

pasterns or between the base of the hoofs (= postdigital, interdigital, and interungulate glands of Owen; fossæ interdigitales of Ogilby; interdigital pits of Hodgson; foot-glands or hoof-glands of other English authors).

Carpal or *knee glands* are the glands commonly represented by a pad of long hair just below the knee or carpus in several Bovidæ.

Tarsal glands are the glands represented by a tuft or pad of hair on the inner side of the tarsus of some telemetacarpal Cervidæ (= the calcic tuft or gland of Hodgson, at least in part).

Metatarsal glands are the glands represented by a pad or tuft of hair on the outer side of the metatarsus of some Cervidæ and of *Epyceros* amongst the Bovidæ (= the calcic tuft or gland of Hodgson, at least in part).

Preorbital glands are the glands in front of the eyes (= suborbital and maxillary pits of Owen; sinus lacrymales and glandulæ maxillares of Ogilby; eye-pits of Hodgson; antorbital glands of other English writers).

Inguinal glands are the saccular glands of the groin (= inguinal pits of Owen; folliculi inguinales of Ogilby; inguinal glands and pores of Hodgson; groin-glands of other authors).

In addition to these there are glands of less common occurrence, such as the *post-cornual glands* of *Rupicapra*, the *occipital glands* of *Camelus*, the *caudal glands* of *Capra*, the *preputial gland* of *Moschus*, and the *unguicular glands* or glands in the false-hoofs of *Tetraceros*.

Part II.—ON THE STRUCTURE OF THE GLANDS AND THE SYSTEMATIC RESULTS TO BE DERIVED FROM THEM.

Family BOVIDÆ.

The subjoined dichotomous analytical key, based mainly on the structure of the feet and upon the specialised cutaneous glands, shows the subfamilies into which the Bovidæ may be provisionally divided on the evidence supplied by these characters. I have preserved all the subfamilies already established by previous authors, and have added a few new ones for the reception of isolated genera which I found could not be included in the divisions to which they had been heretofore assigned without frustrating the attempt to define the groups in question.

The erection of new subfamilies for the accommodation of these aberrant genera appeared to me to be the most expedient course to follow under the circumstances, although some authors may perhaps demur to the separation thus entailed of *Pantholops* from the Antilopinae and of *Oreotragus* from the Neotraginae. Furthermore, I am inclined to think that additional groups of subfamily rank will probably be established in the future. *Boselaphus* and *Tetracerus*, for instance, might perhaps be

wisely and advantageously separated from the African Tragelaphines. Possibly a special subfamily should be erected for *Ammodorcas*, which at present I am unable to classify; and a good case could be made out for splitting up the Rupicaprinae, which no one can claim to be a homogeneous unit. But our knowledge of the mutual affinities of the various sections of the Bovidae is so surprisingly incomplete that no attempt at a final classification of them can at present be attempted.

Owing to the impossibility of arranging the subfamilies according to their probable relationships in a linear series, it comes about that in the annexed table divisions of this rank are juxtaposed which have obviously no near relationship to each other. *Oreotragus*, for instance, is probably, as is usually supposed, allied to the Neotraginae and *Pantholops* to the Saiginae, Antilopinae, or Caprinae. Yet these two genera fall, by the differential characters made use of, under the heading *J'* alongside the *Æpycerinae*, the *Oryginae*, and others with which they have certainly, as I at present believe, no close connection. That is one of the obvious defects of such tables as the subjoined, which are commonly much more useful than scientific.

I have made no attempt to include *Oribos* in this key, Lönnberg's recent paper on this form making one conclusion abundantly clear, namely, that the genus must for the present be left by itself in the subfamily *Ovibovinae*.

- a. On the front and usually also on the hind leg a large interdigital cleft, forming a gland the orifice of which is a long slit with its upper margin sharply defined by the abrupt descent of the integument between the digits; or else the orifice of the cleft is shorter and the gland more or less tubular, extending up between the bones of the pastern, its posterior wall being formed by a close fold of integument forming the heel-tie inferiorly, so that the orifice of the gland opens downwards between the hoofs.
- b. Preorbital gland nearly halfway between the eye and the nose, not valvular or invaginated, but marked externally by a bare streak of skin studded serially with pores; web of pastern reaching only to the heels, closely folded, the gland tubular with the orifice opening freely into the space between the hoofs CEPHALOPHINE (p. 867).
- b'. Preorbital gland occasionally aborted, when present usually a valvular invagination, never marked externally by a streak of integument with serially arranged pores.
- c. Glands equally or approximately equally developed on both front and hind feet.
 - d. Muffle large, naked above as far back as the posterior angle of the nostrils NEOTRAGINÆ* (p. 879).
 - d'. Muffle small, hairy above almost or quite to the anterior angle of the nostrils.
 - e. Pedal glands more or less tubular; the integument of the back of the pastern closely folded at the heels. MADOQUINÆ (p. 876).

* Based upon observation of *Ourechia* and *Raphicercus*, the other genera being unknown to me.

e'. Pedal glands a deep cleft with a long aperture on the front of the pastern, the web extending forwards as a close fold of integument from the heels towards the front of the hoof and separating the cavity of the gland from the space between the hoofs.

ANTILOPINÆ (p. 887).

e'. Pedal glands aborted or nearly so on the hind feet.

BUBALINÆ (p. 900).

a'. Never a deep interdigital cleft opening by a long orifice, with sharply defined upper margin, on the front of the pastern; pedal glands when present and well developed somewhat flask-shaped with a constricted orifice opening on the front of the pastern above the hoofs (exc. *Rupicapra*), never opening deep in the interdigital cleft above the heels.

f. A depression on the lower half of the pastern in front caused by the gradual downward and backward descent of the skin of the middle line towards the heels, where it meets the posterior skin to form the heel-tie, allowing the hoofs to be widely or moderately widely separated apically; only rarely (in *Rupicapra*) does the closely folded integument extend forwards from the heels and shut off the interdigital cleft from the space between the hoofs; pedal gland, when specialised, folded upon itself and opening by a small orifice on the front of the pastern high above the hoofs.

RUPICAPRINÆ* (p. 848) and CAPRINÆ (p. 859).

f'. At most a shallow depression on the front of the pastern; the hoofs joined together almost throughout their basal extent by an interungual band of integument extending forwards from the heels, where it meets at an obtuse or right angle the skin forming the posterior wall of the pastern; it similarly meets that of the anterior wall of the pastern, which forms a continuous surface in the middle line, except where its continuity is sometimes broken for a short distance by the orifice of the pedal gland, which, when present, opens close to the hoofs; thus, except for the glandular infolding, the anterior and posterior walls of the pastern are widely separated from each other in the middle line.

g. Hoofs truncated apically, the heels raised high above the ground during progression: (interungual integument hairy throughout; a valvular preorbital gland; muffle large; no pedal glands)..... OREOTRAGINÆ (p. 885).

g'. Hoofs pointed, the entire sole and heel in contact with the ground during progression.

h. Nasal cavities considerably inflated; skin of the heel-tie posteriorly folded upon itself in correlation with the backward extension of the enlarged heels: (no preorbital or pedal glands; a pair of very large inguinal glands with orifice remote from the mamma)..... PANTHOLOPINÆ (p. 898).

h'. Nasal cavities not specially inflated; skin of heel-tie not folded, heels moderate in size.

i. A pair of large metatarsal glands on the hind legs; no false hoofs; interungual integument continuously hairy; [no preorbital or pedal glands].

ÆPYCÉRINÆ (p. 918).

* This section should, perhaps, be divided into two or more subfamilies, none of the genera being closely related to one another. *Saiga* should possibly come under the heading *f* as the type of a special group *Saiginae*; but the exact structure of the feet and of their glands is unknown to me.

i'. No metatarsal glands; false hoofs present; interungual integument naked.

k. Pedal glands present on all four feet and consisting of a thick-walled, elongated sac gradually lessening in calibre towards the orifice, which is situated close to the summit of the interungual web; or else the gland is small and opens behind a conical excrescence developed from the summit of the interungual web as in *Addax** ORYGINE (p. 907).

k'. Pedal glands absent, except in *Pelea*, where they consist of a thin-walled, compressed, roundish sac with a short and narrow neck, the orifice of which opens some little distance above the summit of the interungual web CERVICAPRINE (p. 911).
TRAGELAPHINE (p. 921), BOVINE † (p. 932).

Subfamily RUPICAPRINÆ.

Genus RUPICAPRA Blainv.

RUPICAPRA RUPICAPRA Linn. (The Chamois.)
(Text-fig. 83.)

According to Owen the Chamois has no preorbital glands, but possesses inguinal glands and a gland behind the base of each ear. Mr. Lydekker, on the contrary, states that a small preorbital gland is present ‡; and even so recently as 1904 Max Weber ('Die Säugethiere,' p. 675) asserts that the male possesses postauricular glands. The pedal glands were described by Max Tempel.

Living examples of Tyrolean Chamois in the Zoological Gardens show no trace either of the preorbital gland mentioned by Mr. Lydekker or of the post-auditory gland mentioned by Owen and other writers; nor could I detect a trace of them in the only fresh specimens I have been able to examine, namely two newly born kids, or upon dried skins in the British Museum.

The feet of these immature specimens were more like those of Gazelles than of any Antelopes, Sheep, or Goats that I have seen. When the hoofs were pulled apart a triangular interdigital depression was shown. This, however, was both shorter and much shallower than in Gazelles. It became gradually shallower and narrower upwards to its apex, the deepest and broadest part being at its lower end, where it was closed by the interungual web. The skin of this web was folded back in the same way as in Gazelles, but much less deeply, so that the skin forming the back of the glandular depression was separated some distance from that of the back of the pastern. The walls of the depression were somewhat scantily clothed with short hairs. Also, as in Gazelles, the entire interungual web, extending from near the

* On account of the peculiar structure of the feet this genus should perhaps form the type of a special subfamily, Addacinae.

† These groups are distinguishable by other characters than those supplied by the feet.

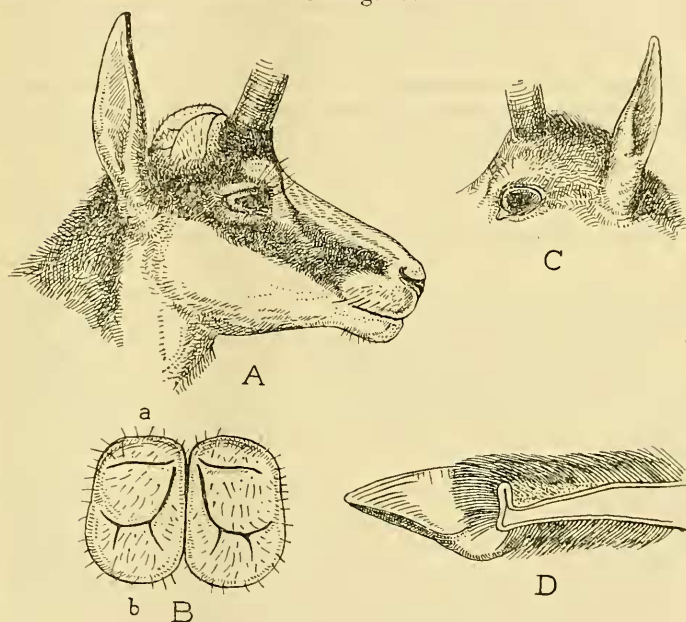
‡ 'Great and Small Game of Europe,' p. 173, 1901. The authority for this statement is not given.

front of the proximal end of the hoof almost to the heels, was clothed with long hairs, the heel-tie itself being naked.

The feet of these immature specimens agreed with those of an adult Chamois described and figured by Max Tempel (*op. cit.* p. 50, pl. xi.), except for the more scanty clothing of hairs on the walls of the depression. In Max Tempel's example the walls of the depression were thickly clothed with long hairs loaded basally with secretion, and the skin forming the posterior wall of the depression was in contact with that of the back of the pastern as in Gazelles.

Judging from the immature examples above mentioned and from dried skins examined in the British Museum, Chamois have four mammae, but no inguinal glands.

Text-fig. 83.



Rupicapra rupicapra.

- A. Head of male showing fully developed postcorneal glandular swelling.
- B. The glandular swelling from above: *a*, anterior, *b*, posterior end.
- C. Summit of head of adult female drawn on the same day as A, showing absence of swelling.
- D. Foot of newly born kid showing depression on the front of the pastern.

That Chamois possess glands upon the head has been known for many years. These glands have had a curious and confusing history. They have been persistently described as "post-auditory" or "post-auricular," whereas in reality they are immediately

behind the horns and well in advance of the base of the ears. By no possibility can they be described with accuracy as behind the ears. I think Hamilton Smith must have been the first to start this error in 1827. In Griffith's 'Animal Kingdom,' iv. p. 22, he stated that there was a gland behind the ear; but on p. 281 of this volume he described the same gland apparently as occurring behind the horns. In 1836 Owen repeated the statement that they are post-auditory, thus confirming my suspicion that he borrowed many of the facts for his paper from Hamilton Smith. In 1855 the glands were quite correctly figured and described by Von Hessling as behind the horns (Zeitsch. f. w. Zool. vi. pp. 265-271, pl. viii.); but in the illustration accompanying this memoir the ears appear to have been added as an afterthought, for they are drawn as projecting from the side of the head-skin much too far forwards, the anterior edge of their bases being in a line with the posterior base of the horns, so that part of the gland, at all events, is behind the ears. The figure, however, is quite wrong in that particular. As is well known, the horns of a Chamois rise vertically nearly over the eyes and the ears are set far behind both. To Owen's mistake and Von Hessling's inaccurate figure must probably be attributed the statement made by Flower and Lydekker ('Mammalia,' p. 12, 1891), by Max Weber (Die Säug. p. 675, 1904), and by Lydekker ('Field,' 1909, p. 1100) that the glands in question are post-auditory, the latter even speaking of them as "occipital." Yet, curiously enough, Flower knew at one time that they were behind the horns and in front of the ears, because there is a preparation in the Museum of the College of Surgeons showing their exact position; and in the catalogue there is an entry in his handwriting, giving an accurate description of the preparation with a reference to von Hessling's paper*. This specimen was received from the Zoological Society in 1877, many years before the repetition of Owen's mistake by Flower in his classical work on the Mammalia.

A further point of interest connected with this specimen is that it was a female. The glands appear as a pair of subcrescentic slits, one behind each horn and about half an inch away from it. This establishes the conclusion that the female possesses the glands as well as the male, although they do not appear to become enlarged at the breeding-season as in the latter. Their appearance in the bucks was recently described by Mr. A. Buxton ('Field,' 1909, p. 1056), who found them in the autumn of the year in various stages of growth, and said that they gave out a strong goaty smell.

In the male Tyrolean Chamois now living in the Gardens the glands began to swell in the latter half of September when the coat began to darken, were at their maximum through November and the first half of December, then gradually dwindled away, and by the end of the first week of January were represented by a flat

* I am indebted to Mr. R. H. Burne, F.Z.S., for this information.

area of wrinkled skin buried in the hairs of the top of the head. At no time did I see any discharge or secretion coming from them. At their best they projected well above the longest hairs on the parietal area of the head as a pair of rounded cushion-like excrescences of purple skin studded with short hairs and folded into deep intersecting grooves, recalling a pair of cerebral hemispheres marked with a few sulci. Seen from above, the margin is straightish in front up against the horn, lightly convex externally, widely rounded posteriorly, and straight internally, where it is closely in contact throughout its length with that of the opposite side. The surface is convex from before backwards and from side to side; and from the antero-internal angle of each on the upper side two deep sulci descend towards the external border, one close behind the horns, the other backwards and outwards, giving off two backwardly-directed short sulci in its course.

In a male eighteen months old the glandular area showed no signs of swelling as late as November.

In one of the newly born kids I found these postcornual glands represented by a pair of very shallow crescentic grooves entirely concealed in the hairs of the top of the head.

Genus OREAMNOS Raf.

OREAMNOS MONTANUS Ord. (The Rocky Mountain Goat.)

(Text-fig. S4, A.)

The presence of glands behind the horns in this species has been recorded by Mr. Hornaday*, Mr. Frederick Gillett†, and by Mr. Madison Grant‡. Mr. Hornaday described them as "a peculiar bare patch of black oily skin, the size of a half dollar." To this Mr. Gillett added the important information that "under the external skin these glands consist of a soft red tissue saturated with a milky substance, like the udder of a cow. In the specimen at our [London Zoological] Gardens these glands are partially covered up by long hair at the present time [February], but in October and November they are more conspicuous. The older the animal the more pronounced are the glands." According to Mr. Madison Grant the gland, which is as large as half an orange and situated in a half-circle immediately behind each horn, "is sometimes so tough as to wear deeply into the base of the horn." This author cites the presence of this gland as the most striking character of *Oreamnos* as compared with other genera of *Rupicaprinae*. No doubt his failure to recognise it as the same gland that is found in the Chamois (*Rupicapra*) is to be attributed to the erroneous description of the latter as "post-auricular."

My own notes upon an old male animal living in the Gardens completely bear out what Mr. Gillett said as to the seasonal development of the gland. In this respect it agreed closely with

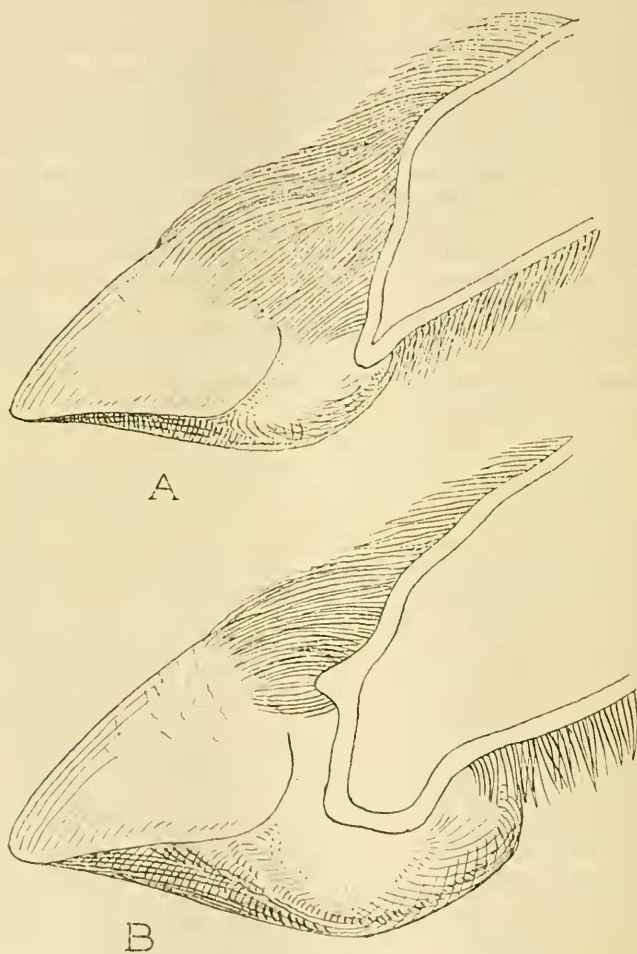
* 'American Natural History,' 1904, p. 115.

† P. Z. S. 1905, vol. i. p. 56.

‡ Ninth Annual Report of the New York Zool. Soc. p. 12 (reprint).

the homologous gland of the male Chamois; but the integument covering the gland was much more horny and coarser in texture than in the Chamois.

Text-fig. 84.



A. Median vertical section of front foot of *Oreamnos montanus*.
B. The same of *Budorcas tibetanus*.

This Rocky Mountain Goat had no preorbital or inguinal glands. The feet were constructed almost as in Goats (*Capra*); that is to say, there was on the lower part of the pastern in front a deep interdigital depression formed by the abrupt downward and backward slope of the integument to meet that of the posterior

side of the pastern at an acute angle just above the heels, firmly binding the latter together. As in wild and most tame Goats, the walls of this depression were clothed with long hairs. On the hind feet these hairs were clean; but on the fore feet they were stained yellow and stuck together, showing dried scurfy material at their roots and suggesting activity of the sebaceous glands over a considerable part of the area.

The genus *Oreamnos* exhibits puzzling cross-affinities. With the feet and beard of the Goats (*Capra*) are combined the short cannon-bones of the Takin (*Budorcas*), the post-cornual glands of the Chamois (*Rupicapra*), and the short, lightly curved, backwardly inclined horns of *Capricornis* and *Nemorhedus*.

Genus *NÆMORHEDUS* H. Sm.

NÆMORHEDUS GORAL Hardw.

(The Goral.)

According to Hodgson, *N. goral* has no inguinal or preorbital glands, but possesses feet-pits on all four feet. Owen is in agreement with him as regards the absence of the glands in the groin and on the face.

Ogilby also states that the preorbital and inguinal glands are absent, and adds that the pedal glands are large and the mammæ four in number.

My own observations agree with these in every respect.

On a flat skin of *N. goral* sent to me from Chamba by Major Rodon, F.Z.S., I found the pedal glands present on all the four feet. They presented a close resemblance both in position and structure to those of Sheep (*Ovis*), opening by a small orifice on the front of the pastern some distance above the hoofs. The orifice led into a slightly dilating hair-lined sac running backwards to the posterior wall of the pastern parallel to the interungual web. Just below the orifice the integument descended obliquely between the hoofs to the heels, where it formed a stout horny tie. This interungual web met the integument of the back of the pastern on the heels almost at right angles. The hair on the back of the pastern extended only for a short distance between the heels; but the interungual integument was covered with long hairs, becoming progressively shorter towards the heel-tie, which was itself smooth and hairless. The hoof itself was short and compressed with the heels high, their web or tie being raised considerably above the ground. Thus not only in the position and structure of the pedal gland*, but also in the hairiness of the interungual integument and the smoothness of the heel-tie, a very close resemblance could be traced between the feet of *Nemorhedus* and those of *Ovis*.

* I believe the pedal gland described above was incomplete, since the bones and tissues of the pastern had been to a large extent cut away from behind and there was a small tear in the skin of the bottom of the gland.

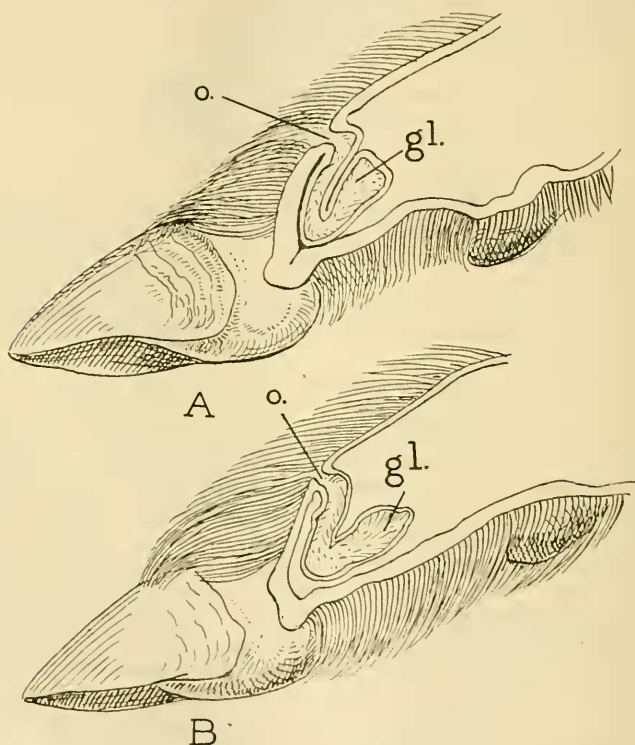
NEMORHEDUS RADDEANUS Heude. (Radde's Goral.)

(Text-fig. 85, A.)

The entire skin of an adult example of this species* from Lao-i-san, near Shensi in Central China, was kindly lent to me by Mr. Edward Gerrard.

The structure of the foot was the same as in *N. goral*, except that the hoofs were rather longer and the pedal gland much

Text-fig. 85.

A. Median vertical section of front foot of *Nemorhedus raddeanus*.B. The same of *Capricornis crispus*.

gl., pedal gland; o., its orifice.

(Dry specimens.)

longer and more capacious. Just within the orifice the duct was directed for a very short distance upwards and backwards. It then took a sharp bend downwards and forwards, running close along the interdigital web to the heel-tie. At this point it was

* Vide Pocock, P. Z. S. 1908, p. 196.

bent sharply backwards and upwards on itself, the terminal portion which, roughly speaking, ran parallel with the integument of the back of the pastern, being subequal in length to the portion running parallel to the interungual web. The gland was lined with hairs and charged with secretion. Its structure was practically the same on both front and hind feet.

There were two pairs of teats, but no trace of inguinal glands could be detected.

Genus CAPRICORNIS Ogilby.

CAPRICORNIS THAR Hodgs.

(The Nepalese Serow.)

According to Owen this species possesses preorbital glands, but is without inguinal glands. Ogilby, however, asserts that it has inguinal glands and pedal glands and four mammae.

In the example of the Darjiling race (*C. thar jamrachi* Poc.) *, now living in the Gardens, a distinct but small orifice is observable upon the pastern of the fore foot, and the white hair immediately around it is at times stained yellow, proving that a gland is present and active. This animal is a female nearly five years old; and the preorbital gland is never prominent or turgid as described by Hodgson in the case of the male *C. thar* †. It is represented externally by a circular orifice, from which exude drops of whitish fluid hardening into solid particles, recalling both the appearance and scent of gum arabic. I am unable to state anything about the inguinal glands.

CAPRICORNIS (or CAPRICORNULUS) CRISPUS Temm.

(The Japanese Serow.) (Text-fig. 85, B.)

Mr. Edward Gerrard kindly lent me a dried skin of this species.

The preorbital gland consisted of a simple hair-lined pouch with a small subcircular orifice. The pedal glands were well developed on all four feet, and resembled almost exactly in structure those of *Nemorhedus raddeanus*. The feet also were constructed as in that species, though the hairy clothing was longer. There were four teats, but no inguinal glands.

I am also indebted to Mr. E. Gerrard for the opportunity to examine the flat skin of a female of *C. argyrocheates* from Szechuen. On this I could find no pedal glands except a shallow depression on one of the anterior feet, recalling the aborted pedal glands of *Capra*, *Pseudois*, and *Hemitragus*. Moreover, the hair on the front of the pastern did not extend so far downwards between the hoofs as in *C. crispus* and *Nemorhedus raddeanus*. The state of preservation of the feet on this skin does not justify the final

* Abstr. P. Z. S. no. 55, p. 12, 1908; P. Z. S. 1908, p. 183, fig. 34.

† P. Z. S. 1836, p. 39.]

conclusion that the glands are absent; and until more is known of the pedal glands of the other species referred to *Capricornis*, no certain conclusions can be drawn regarding the taxonomic value of the facts above recorded. If *C. argyrochates* prove to be without glands and *C. thar* to have them, there will be a strong *prima facie* case for regarding these species as belonging to two distinct genera. *C. thar* is the type of *Capricornis*, and for *C. argyrochates* the name *Nemotragus* Heude will have to be employed.

Finally, it may be added that Owen states that *C. sumatrensis* possesses inguinal glands as well as the preorbital glands—a fact which still further emphasises the importance of the examination of fresh material of this little-known genus.

Genus BUDORCAS Hodgs.

BUDORCAS TAXICOLOR WHITEL.

(The Bhutan Takin.)

In the living example of this Takin in the Gardens there is no trace of preorbital gland, and none of pedal glands on the fore feet, as may be clearly seen when the animal rears herself up with the hoofs spread against the bars.

BUDORCAS TIBETANUS M.-Edw. (The Chinese Takin.)

(Text-fig. 84, B, p. 852.)

Mr. Gerrard kindly allowed me to cut the fore and hind feet of a female example of this species from Szechuen. There was no trace of pedal glands on either the fore or the hind feet. On the fore feet the integument on the anterior surface of the pastern ended in the middle line below in a strong transverse web, beneath which it passed between the hoofs nearly parallel with the proximal edge of the inner surface of the nail, then turned sharply at right angles, forming a strong heel-tie running parallel with the sole of the hoof before turning up to be continued with the skin of the back of the fetlock. As in the Serow (*Capricornis argyrochates*) practically the whole of the interdigital integument was naked, although anteriorly the hair on the front of the fetlock was continued a little lower, slightly below the transverse web. The hoofs themselves were shaped very much as in *Capricornis*, but the heel-tie was situated more forwards and nearer the proximal edge of the inner lamina of the nail, making the hoofs much less distensible than in that genus.

The structure of the hind foot was essentially the same as that of the front foot, but there was no trace of the anterior integumental web.

There was no trace of inguinal glands, but the four teats on the dried skin were curiously invaginated, giving the appearance of four small symmetrically arranged pits, which I at first mistook for inguinal pouches.

The genera of Rupicaprinae may be distinguished as follows by their cutaneous glands:—

- a. Muffle large, encircling the nostrils below and extending as far as their posterior angle above; a well-developed pedal gland like that of *Ovis* on all four feet.
- b. Preorbital glands present *Capricornis*.
- b'. Preorbital glands absent *Næmoredus*.
- a. Muffle small; pedal glands, when present, otherwise formed.
- c. A pair of glands behind the horns in both sexes; interdigital cleft deep.
- d. Interdigital glandular cleft opening inferiorly between the hoofs, the heel-tie simple *Oreamnos*.
- d'. Interdigital cleft shut below by a close fold of integument extending forwards from the heels towards the proximal margin of the nail in front *Rupicapra*.
- c'. No glands behind the horns; interdigital cleft shallow *Budorcas*.

Subfamily OVIBOVINÆ.

Genus OVIBOS Blainv.

OVIBOS MOSCHATUS Linn. (The Musk-Ox.)

(Text-fig. 86.)

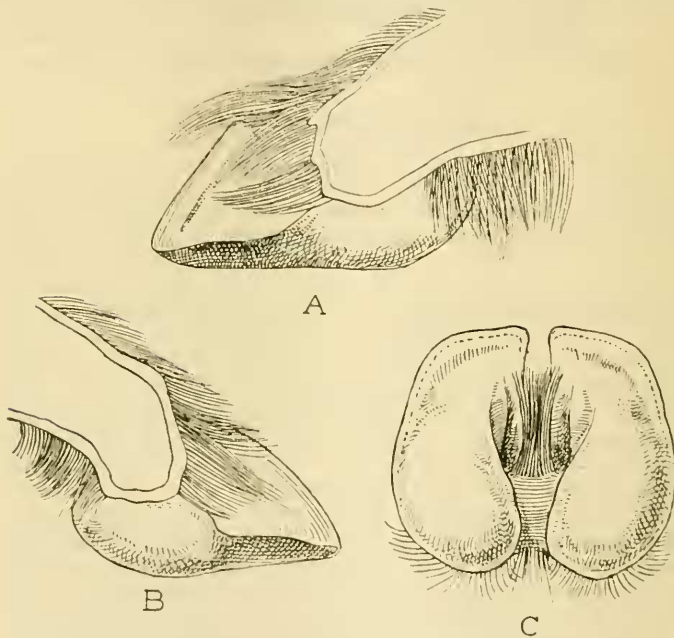
According to Ogilby this animal has four teats, but neither preorbital nor inguinal glands. Of the pedal glands he said nothing. Lönnberg (P. Z. S. 1900, pp. 163-165) agrees as to the number of teats and apparently as to the absence of inguinal glands; but he found in his specimen the preorbital gland well developed, being 23 mm. long, 18 mm. broad, and 8 mm. deep. The interior of the pit was lined with hair, but I cannot judge from the description whether the orifice was valvular as in *Ovis* or simple as in *Capricornis* (the Serow).

Lönnberg also states that he failed to find any pedal glands. I was able to verify this fact on a front and a hind foot of a Musk-Ox which Mr. E. Gerrard kindly allowed me to cut. On the fore foot the skin of the middle line of the pastern in front ends inferiorly in a small web, beneath which the integument runs backwards and downwards to the anterior portion of the heel, then curves upwards and backwards towards the posterior portion of the heel, where it is continuous with the skin of the posterior surface of the pastern. This skin is covered with long hairs, which pass for a short distance between the heels, but the greater part of the integument which ties the heels together is quite naked. Above the heel-tie, however, the interungual integument is covered with long hairs, which largely overlap the proximal inner margin of the nail; and when the hoof is examined from below these hairs appear as a long and thick tuft projecting forwards from the anterior portion of the heel-tie and filling the greater part of the interungual space. Long hairs arising from the bottom of the pastern in front also overlap the proximal anterior portion of the hoof. As is well known, the hoofs are remarkably short

and broad, the antero-external portion of the nail being enormously developed as compared with the small internal portion, the soles and heels being correspondingly large.

The hind foot is very like the fore foot, and has no trace of a gland; nor on the specimen examined did I find any trace of the small antero-superior web, and the integument of the front of the pastern descended more abruptly between the hoofs down to the heels, making a more marked depression between the hoofs than was visible before the front hoof.

Text-fig. 86.



Oribos moschatus.

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Lower surface of hind hoof.

The systematic position of *Oribos* must for the present be left unsettled. According to Lönnberg, it should rank as a special subfamily, for which the name *Ovibovinae* is retained. Gray*, it may be added, long ago placed the Takin (*Budorcas*) with *Oribos* in the family *Ovibovidae*; but the evidence that the two are really related is not convincing, and cannot be settled until the anatomy of *Budorcas* is known.

* Cat. Rum. Mamm. in the British Museum, p. 31, 1872.

Subfamily CAPRINÆ.

Genus OVIS L.

(Sheep.)

Ogilby stated that in *O. aries* (Domesticated Sheep) the preorbital glands are large but immovable, the pedal glands small and the inguinal glands absent, adding that there is only a single pair of mammae.

According to Hodgson, *O. ammon*, the Siberian Argali, and *O. ammon hodgsoni* (= *ammonoides*), the Tibetan Argali, have large but immovable preorbital glands, distinct inguinal glands, and pedal glands on all four extremities, whereas *O. musimon*, the Mouflon, for which on that account he created the genus *Caprovius*, differs in having no pedal glands.

Owen ('Anatomy of Vertebrates,' iii. p. 638, 1868) described and figured the pedal gland presumably of a domesticated breed; but according to Isidore Geoffroy the glands are absent in some breeds; most modern text-books and systematic treatises state that the preorbital, pedal, and inguinal glands are present, and that there is a single pair of mammae, a statement with which my own observations are entirely in accord except that there is occasionally an additional pair of small mammae.

I have examined fresh specimens of two wild species, namely, *O. vignei* and *O. musimon*, and a dried skin of *O. canadensis*.

OVIS VIGNEI Blyth. (The Urial or Gad.)

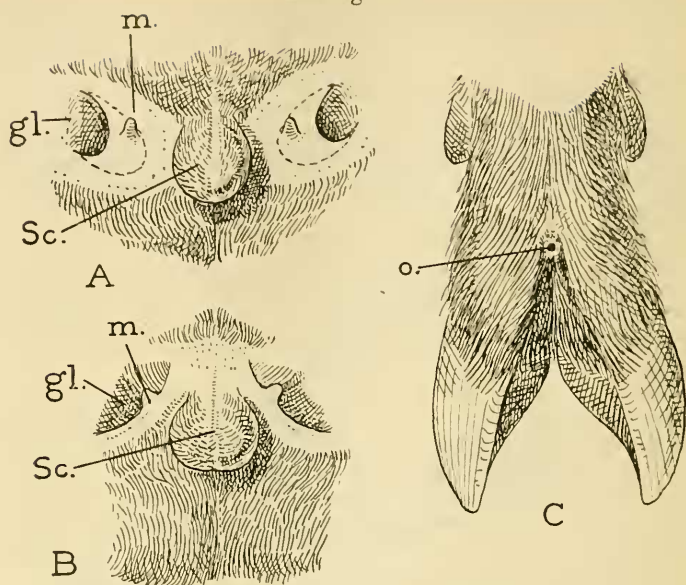
(Text-figs. 87, 88.)

The preorbital gland consists of a hair-lined valvular pocket or invagination closed by a flap of skin forming a movable upper lid. The pocket in captive specimens is commonly blocked with a nearly dry and waxy or quite dry secretion with no definite smell but that of "sheep," and the hairs around the orifice are generally stuck together with the same substance. The dryness of the secretion is probably pathological and due perhaps to insufficiency of green or natural food.

The inguinal glands, two in number, consist of rather shallow pouches, with the deep part underlying the teat, close to which the wide suberescenscent orifice opens. The secretion is yellowish and waxy, and gives off a powerful odour, just like that of the urine of the common House Mouse (*Mus musculus*). The area of skin surrounding the teat and gland is naked. Normally there is a single pair of teats. In one specimen, however, I found an additional smaller pair lying in front of the pair adjacent to the orifice of the gland.

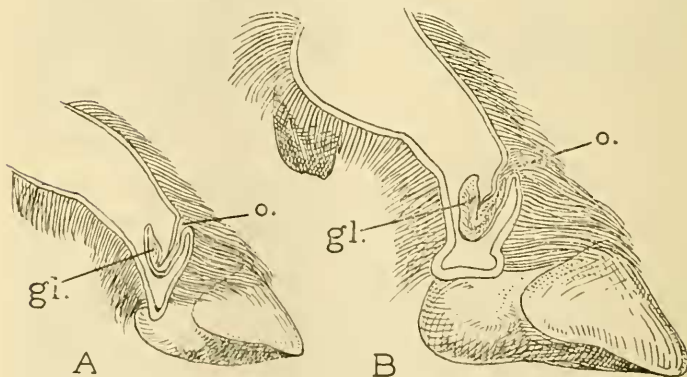
The structure of the feet is very constant. When the hoofs are pulled apart a triangular hairy depression is seen in the middle line of the lower half of the pastern. This depression is caused by the

Text-fig. 87.

*Ovis vignei.*

- A. Inguinal region of young male: *m.*, mamma; *gl.*, orifice of gland, the size of the invagination shown by a dotted line; *Sc.*, scrotum.
 B. The same of lamb three days old, showing the shallow glandular depression (*gl.*).
 C. Front foot of an adult showing the orifice of the pedal gland (*o.*).

Text-fig. 88.

*Ovis vignei.*

- A. Median vertical section of foot of lamb three days old.
 B. The same of adult.

gl., pedal gland; *o.*, its orifice.

somewhat abrupt descent of the integument just above the hoofs. It descends straight down to the heels, which are united by a strong tie running for a short distance parallel to the sole of the hoof before turning upwards in continuation with the skin of the back of the pastern. The heel-tie is the only portion of the interungual integument which is hairless, the area above the tie being covered with long hairs which project forwards, overlapping the proximal margin of the nail in front.

The hoofs are short and pointed and the heels of the hoofs well developed, being both high and long, so that the integumental tie between them is raised considerably above the ground.

The pedal gland opens by a small circular orifice near the summit of the triangular depression on the front of the pastern, some distance above the hoofs. The orifice leads into a narrow duct which quickly but gradually expands into the gland. The latter descends along the interungual integument towards the heel, then turns sharply upwards and backwards upon itself for a short distance along the integument of the back of the pastern.

The gland is lined with short hairs, and the secretion is a clear semi-fluid substance with a pleasant scent like toffee (baked butter and sugar), slightly infused with acetic acid.

Of this species I have examined several specimens of various ages from Persia. One example three days old had all the glands developed, the pedal glands being as large relatively as in the adult, the preorbital gland only a little smaller, but the inguinal glands decidedly shallower. I have also noticed that the inguinal pouches are sometimes quite shallow in Sheep of domesticated breeds.

OVIS MUSIMON Schr.

(The Sardinian Mouflon.)

This species has the glands of the same structure as in *O. vignei*, with the preorbital gland smaller; but in one specimen I noticed an unexpected difference in the feet, the entire interungual area from a point on a level with the front of the hoof downward including the heel-tie being naked instead of hairy.

OVIS CANADENSIS Shaw.

(The Rocky Mountain Bighorn.)

In a dried skin of this species, for which I was indebted to Mr. E. Gerrard, I found the preorbital gland, which Mr. Lydekker has described as minute and almost rudimentary, to consist of a small but very distinct valvular invagination, only differing in its relatively smaller size from that of other species of Sheep. The presence of a pair of inguinal glands was unmistakably indicated and there was a single pair of teats. Remains of the pedal glands showed that these organs open as in ordinary Sheep, and the interdigital area was clothed with hair down to the heel-tie.

Domesticated Sheep.

Of Domesticated Sheep I have examined examples of many breeds from different countries without finding any variations of moment in the structure of the pedal, inguinal, or preorbital glands. The rarest specimens were the following:—a lamb of three or four months old from Fair Island between the Orkneys and Shetlands, belonging to Mr. A. J. Sewell; a black lamb of about two months old, probably belonging to a four-horned breed from Caithness in Scotland; an adult short-tailed ram of the breed from the island of Soa in the Hebrides; a Humia or Fighting Ram from Nepal and a four-horned breed from the same country, both short-tailed; two rams of the long-tailed maned breed belonging to the Haussa tribes of N. Nigeria; and a fat-tailed South-African Sheep belonging to Sir Claud Alexander*.

In three of these sheep, namely, in the Caithness and Soa specimens and in the Humia Ram, I noticed that the interungual area was hairy, exactly as in *O. vignei*, and not naked as in the example of *O. musimon* described above.

In no Sheep, domesticated or wild, have I found the pedal glands absent; and in every case where the scent of the secretion was tested it had the sweet odour of toffee. The histology of the pedal glands of *Ovis aries* has been fully described by Max Tempel.

Genus AMMOTRAGUS Blyth.

AMMOTRAGUS LERVIA Pall. (=OVIS TRAGELAPHUS).

(The Barbary Wild Sheep.)

I have had no opportunity of examining a dead specimen of this species; but careful inspection of a living male example gave the following results.

There was no trace of preorbital gland. Inguinal glands also were absent, and there was a single pair of teats. The feet were constructed as in Sheep and Goats; but there was no trace, either upon front or hind feet, of any orifice leading into a special gland such as is present in Sheep. In Sheep the orifice of this gland may be seen at once by superficial scrutiny of the front of the pastern, in spite of the hairy clothing. The most striking peculiarity about the feet of this example of *O. lervia* was the apparent smoothness of the interungual integument and the

* It is commonly stated in works on Natural History that domesticated breeds of Sheep differ from all the wild species in having long tails. This is not true. Of the above-mentioned Sheep the shortest tail, containing only 5 vertebrae with a short terminal unsegmented portion, was found in the Soa breed. The Fighting or Humia Ram from Nepal had a tail $6\frac{1}{2}$ inches long, containing 10 vertebrae. In the Caithness breed the tail scarcely reached the hocks and contained 15 vertebrae. In the Haussa Sheep, on the contrary, the tail nearly reached the fetlocks and was composed of 20 vertebrae, as in a fat-tailed Asiatic Sheep mentioned by Pallas. It may be added that Nepalese Sheep of the Humia, four-horned, and one-horned races all have short tails, the tail of an adult four-horned specimen measuring only $3\frac{1}{2}$ inches.

shortness of the hairs clothing the interdigital depression on the front of the pastern.

In the absence of preorbital, of inguinal, and of specialised pedal glands *Ammotragus lervia* agrees with *Pseudois*, *Hemitragus*, and *Capra*, and differs from *Ovis*. The glands, in fact, completely bear out the conclusion suggested by the structure of the skull and certain external features described in text-books, that *Ammotragus* cannot consistently be included in *Ovis* if *Capra* be excluded therefrom.

I do not know who was the authority for the statement found in Mr. Lydekker's work 'Wild Oxen, Sheep, and Goats,' pp. 149 & 226, 1878, that this animal possesses pedal glands. The invariable presence of these glands is cited as characteristic of *Ovis* as contrasted with *Capra*; and the species in question is included under *Ovis*, although subgeneric rank is assigned to it.

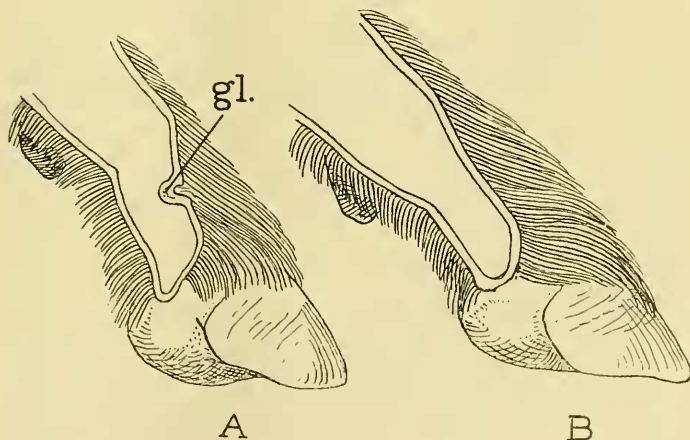
Genus PSEUDOIS Hodgson.

PSEUDOIS NAYAUUR Hodgson. (The Bharal.)

(Text-fig. 89.)

According to Hodgson, *O. nayaur* has no preorbital glands, but possesses small pedal glands on all four feet and two inguinal glands, marked, however, by vague pores. It was principally on

Text-fig. 89.



Pseudois nayaur.

- A. Median vertical section of front foot of female retaining the aborted gland (*gl.*).
 B. The same of the male without trace of the gland.

the absence of the preorbital glands that Hodgson separated this species from *Ovis* as the type of a distinct genus *Pseudois*. Blanford repeats the information supplied by Hodgson, but without quoting him as his authority.

I have examined two fresh examples, male and female, of this species, and can endorse what Hodgson says with regard to the absence of the preorbital gland, though its position was marked by a small patch of naked skin. I found, however, no trace of inguinal glands, and Hodgson himself admits that the pores (invaginations) are "vague." Perhaps the glands he found were mammary glands. As for the pedal glands, I discovered on the fore feet of one specimen (a female) a very small invagination dipping into a subcutaneous glandular patch, exactly like the gland described above as occasionally occurring in Goats. On the hind feet a similar small pocket was present, but there was apparently no differentiated gland. In a full-grown male there was no trace of the gland or the invagination on any of the feet. Except that the interdigital depression is perhaps a little shallower, the feet do not differ structurally from those of Goats. The depression is covered with long hairs, the tips of which overhang the margin of the nail; only the bridge of skin holding the heels together is naked. The practical suppression of all the glands found in typical Sheep is, in my opinion, ample justification for regarding the Bharal as the type of a genus distinct from *Ovis*, quite apart from other structural differences such as those supplied by the skull. Whether or not *Pseudois* can be distinguished from *Capra*, to which it is linked by one of the races of *C. cylindricornis*, is another matter.

Genus CAPRA Linn. (Text-fig. 90, B.)

All authors seem to agree that the preorbital and inguinal glands are invariably absent in this genus; but there is no such unanimity as regards the pedal glands. According to Ogilby they are present; whereas Hodgson says they are either altogether wanting, or present only on the fore feet, and Isidore Geoffroy* states that they are very rarely present. Hodgson records their occurrence on the fore feet in specimens of three distinct breeds of domesticated Indian Goats, namely the Chyapu, the Sinal, and the Dúgú. He gives, moreover, an illustration of an extracted gland, which shows it to be of the same general structure as in Sheep, although relatively smaller†.

Having examined the feet of many English Goats killed in the Society's Gardens for food, I can endorse the accuracy of Hodgson's statement that the glands are absent in the hind feet and present or absent in the front feet. In the latter, however, they are much more commonly absent than present, and I have never found them so well developed as Hodgson represents‡. They are, when present, represented by a shallow pocket-like invagination bearing a few short hairs, those that protrude from the orifice being stuck together with secretion. This invagination

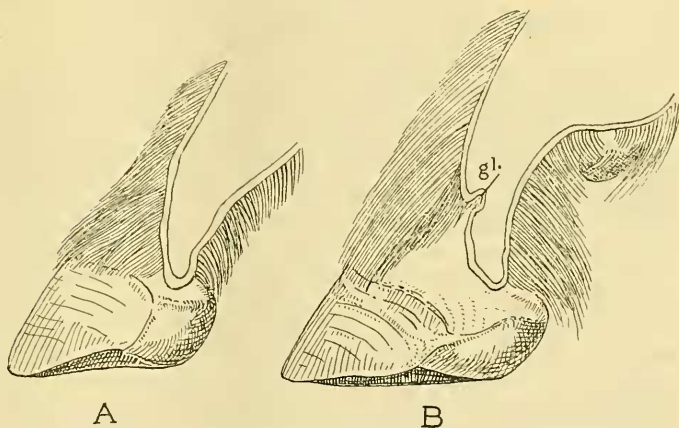
* Hist. Nat. gén. iii. p. 435.

† J. A. S. Bengal, xvi. pt. ii. pp. 1016-1026, 1847.

‡ Max Tempel also only occasionally found an aborted gland in Domesticated Goats.

occupies the same position as the orifice of the gland in *Ovis*; and this fact, coupled with the close resemblance that Hodgson showed to exist between the glands of *Capra* when well developed and those of the former genus, suggests that the ancestors of existing Goats had glands on the fore feet, and probably also on the hind feet, like those of Sheep. The feet themselves also closely resemble those of Sheep. There is a deep depression between the penultimate phalanges, formed by the abrupt downward slope of the integument of the upper (anterior) side to meet that of the lower side at an acute angle just above the heels, forming a strong sometimes horny union between them. The heels are thus incapable of much distension, whereas the tips and proximal portion of the upper side of the hoofs can be widely separated. The heels are

Text-fig. 90.



A. Median vertical section of front foot of *Hemitragus jemlaicus*.

B. The same of *Capra hircus* (var. dom.) retaining aborted pedal gland (*gl.*).

high and prominent behind. So far as the hairiness of the interdigital depression is concerned, great variation exists. In some cases it is covered with longish hairs, in others it is quite naked, an intermediate condition existing in others. Seeing how constant a specific character the hairiness of this area is in wild species of Ruminants, I am at a loss to know what explanation to put upon its variability in these domesticated animals, which are supposed to be descended from *C. agagrus*.

Domesticated Goats have two shallow glandular pouches at the base of the tail beneath, one on each side, close to the anus. I have also found these in *Capra cylindricornis* and *falconeri*.

Of species usually referred to *Capra* I have examined the following specimens, in addition to the domesticated examples alluded

to above, and found no trace of preorbital, inguinal, or pedal glands in any of them :—

C. agagrus from Crete : one young male.

C. sibirica from Chamba : one young male.

C. falconeri from N.W. India : two adult males.

C. cylindricornis from the Caucasus : one young male and one female kid that died at birth.

The structure of the feet resembled that of Domesticated Goats, and the interdigital depression was in all cases hairy, but showed no sign of secretion such as was observable in the example of *Oreamnos montanus* described above.

Genus HEMITRAGUS Hodgs.

HEMITRAGUS JEMLAUCUS Hodgs. (The Tahr.)

(Text-fig. 90, A. p. 865.)

According to Hodgson this species has no preorbital, inguinal, or pedal glands. The specimens, three in number, which I have examined bear out this statement, except that in one female example I discovered on the hind feet an abbreviated glandular pocket like that found on the hind feet of a female *Pseudois nayaur*. Sometimes, at least, there are four mammae.

Hodgson included in his genus *Hemitragus*, *H. hylocius* from the Nilgiri Hills; but I cannot find any evidence that he examined a specimen of that species for the points mentioned in his generic diagnosis. He separated *Hemitragus* from *Capra* because of the larger size of the "muffe" or naked skin at the end of the nose, the alleged presence of four teats, and the absence of pedal glands, which he himself admits may be altogether absent in *Capra*. According to Blanford, however, *H. hylocius* has but a single pair of teats, thus agreeing with typical Goats.

Hodgson states that the male Tahr has a strong Caprine odour. It is true that in the winter and early spring the animal smells strongly; but the odour is exactly like that of a Cormorant or Frigate-Bird, and not like the odour of *Capra agagrus* or *falconeri*.

Judged by their glands, the genera of Caprinae fall into two categories, as follows :—

- a. With well-developed preorbital, pedal, and inguinal glands, the latter not always invaginated in domesticated breeds *Ovis*.
- a'. Without preorbital and inguinal glands; pedal glands, when present, represented by a very shallow depression, except in some Indian Domesticated Goats, where glands resembling those of *Ovis* are found on the fore feet.

Ammotragus, *Pseudois*, *Hemitragus*, *Capra*.

Subfamily CEPHALOPHINÆ.

(The Duikers.)

According to Owen the following species of this subfamily have inguinal pits and preorbital glands lodged in a depression of the maxilla:—*Cephalophus silvicultrix*, *grimmii* (= *mergens*, *hurchelli*, *grimmii*), *monticola* (*perpusilla*, *pygmæa*), *maxwelli*.

Two species were examined by Ogilby, namely, *C. monticola*, cited as *Tragulus pygmæus*, and *C. grimmii*, cited as *Sylvicapra mergens*. According to this author *C. monticola* has neither inguinal nor interdigital glands, whereas in *C. grimmii* there are small interdigital glands and distinct inguinal glands, both species having oblong maxillary [preorbital] glands lodged in depressions of the maxilla. Ogilby also records the presence of two pairs of mammae in this genus*.

The preorbital gland is described in most recent systematic works as consisting externally of a bare streak of skin studded with a series of pores and situated some distance in front of the eye of the corresponding side. Weber† describes in detail the histological structure of the gland and the nature of its secretion in *C. pygmæus* [= *monticola*], points out the difference it presents in the male and the female, and gives a list of the species in which he had observed its external form, together with much other interesting matter. The pedal glands do not appear to have been described.

Genus GUEVEI Gray ‡.

GUEVEI MAXWELLI H. Sm. (Maxwell's Duiker.)

(Text-figs. 91, A, & 92.)

In a female example from Portuguese Guinea, presented by Dr. Ansorge, the external streak of the preorbital gland was markedly bent downwards at its posterior end towards the anterior corner of the eye, its lower margin being therefore concave. It was studded with about 25 vertically elongate pores, forming a single series, from each of which a few short hairs arose. With pressure, liquid drops of secretion could be easily squeezed from the pores. The gland itself underlying the bare streak did not

* The specific names *perpusillus* and *pygmæus* have been assigned to the so-called Royal Antelope, *Neotragus pygmæus*; and Selater and Thomas cite *Tragulus pygmæus* of Ogilby in the synonymy of *Neotragus pygmæus*. This view is, I think, incorrect, because Ogilby described the preorbital glands of *Tragulus pygmæus* and of *Sylvicapra mergens* in exactly the same terms as "glandule maxillares oblongæ"; and since *Sylvicapra mergens* is admittedly a Cephalophine, one must infer that Ogilby's *Tragulus pygmæus* also belonged to that subfamily and not to the Neotragineæ. That Owen's *Antelope perpusilla* and *pygmæa* were also Cephalophines is clearly indicated by his placing them with other species of *Cephalophus* in a group characterized by "maxillary" as opposed to "suborbital pits." Moreover, he quotes S. Africa as the locality of *perpusilla*, whereas *Neotragus pygmæus* comes from Liberia.

† Arch. mikr. Anat. xxxi. pp. 507-539, 1888.

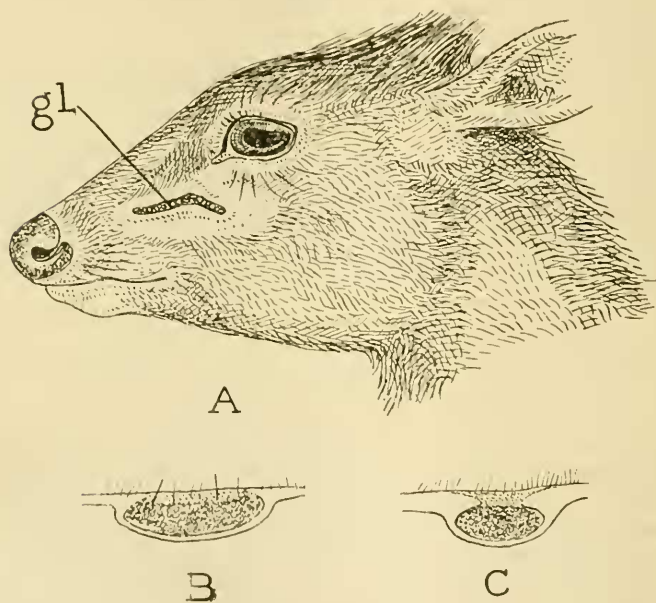
‡ Reasons for the adoption of this genus are given below (pp. 874-876).

differ in structure and consistency from that of *G. melanorheus* and *Sylvicapra coronata* described below. When alive the animal had the habit, not noticed in other Duikers, of rubbing the glandular area against one's hand when presented to her.

There were no inguinal glands, but two pairs of teats were present.

The pedal glands were well developed. The skin of the back of the pastern extended right down to the heels, forming a strong union between them. It was then folded sharply back upon itself, as far as the false hoofs, to form the posterior wall of the gland. At its deepest or upper part the gland formed a laterally

Text-fig. 91.

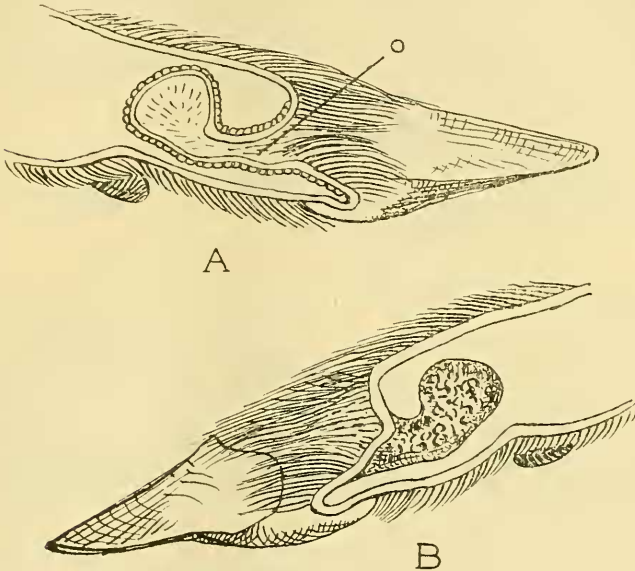


A. Head of female of *Guereza maxwelli*, showing the preorbital gland (*gl.*).
 B. Longitudinal section of the preorbital gland of *Sylvicapra coronata*.
 C. Transverse section of the same.

compressed subcircular sac which communicated with the triangular interdigital depression, seen when the hoofs were pulled apart, by means of a narrow tube with a gradually expanding subcircular orifice. This interdigital depression was formed by the folding back of the skin of the anterior side of the pastern some distance above the proximal margin of the hoof, the infolded portion forming the anterior wall of the gland and constituting a somewhat deep anterior interdigital web which did not project nearly so far inferiorly as the posterior shallower but stronger

web tying the heels together. The walls of the interdigital depression were thickly covered with long hairs projecting downwards over the proximal margin of the nail, those on the anterior side of the posterior web being especially long, so as to conduct the secretion downwards between the heels of the hoofs. The dilated cavity of the glands was beset with short scattered hairs which gradually lengthened towards the orifice of the gland. The secretion itself was white and sticky, with a repulsive odour of dog's faeces mixed with acetic acid.

Text-fig. 92.

*Guevei maxwelli*.

- A. Median vertical section of hind foot: *o*, orifice of pedal gland.
 B. Front foot dissected to show the gland entire.

(Fresh specimens.)

In another female specimen from Sekondi also referred to *G. maxwelli*, the preorbital streak, although lightly concave downwards, was not so abruptly angled at its posterior end as in the one described above. The streak was 18 mm. long, 2 mm. wide, and had a row of about 20 vertically elongated pores, from each of which a few small bristles arose. Drops of fluid could be squeezed in the same way from these orifices. There were no inguinal glands, and the pedal glands resembled those of the first-described specimen.

The absence of the inguinal glands in these two specimens of *G. maxwelli* suggests that Owen was probably wrong in assigning these organs to the species, for it does not seem probable that

such a character is subject to individual variation within specific limits. I suspect, moreover, that Ogilby was correct, and, by implication, that Owen was in error, in stating that inguinal glands are absent in *G. monticola*, since the latter seems to be nearly allied to *G. macwelli*. But I cannot doubt that Ogilby was wrong in saying that pedal glands are absent in *G. monticola*.

GUEVEI AEUATORIALIS Matsch. (Text-fig. 93, A, B.)

The cut foot of a dried skin given to me by Dr. Christy, who shot the animal in the Chagwe forest, Uganda, had a gland of nearly the same structure as in *G. melanorheus*. The foot of this specimen differs in colour from that of *G. macwelli*, being brown all over and showing no white patch just below the false hoofs on the back of the pastern and no white on its front close to the triangular interdigital depression.

The similarity in the structure of their pedal glands favours the view that *G. melanorheus* and *G. aequatorialis* may be subspecifically and not specifically distinct.

GUEVEI MELANORHEUS Gray. (Text-fig. 93, C.)

A single young specimen from Angola presented by Mr. H. F. Varian.

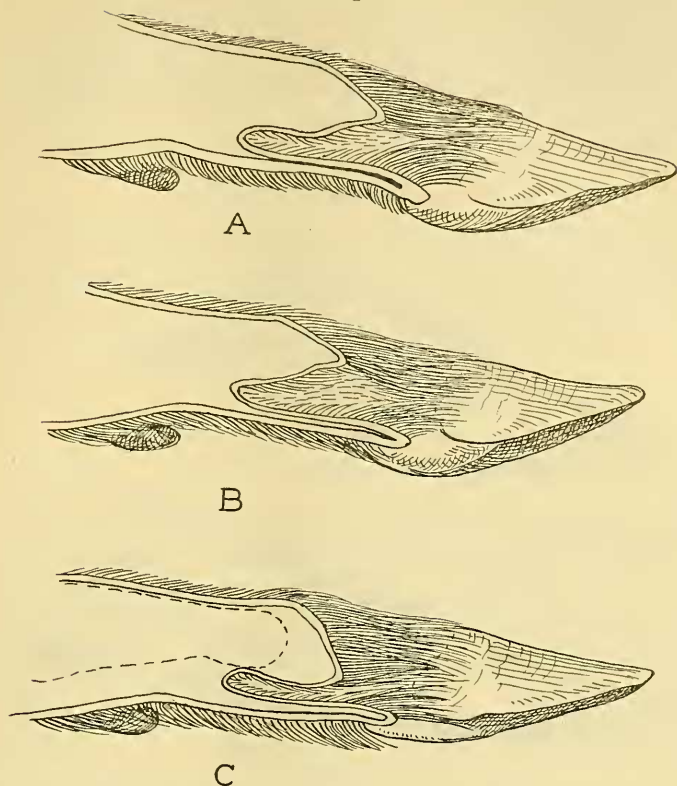
As in *G. macwelli*, the preorbital streak was lightly concave below, but its curvature was less abrupt and situated farther forwards than in Dr. Ansorge's example from Portuguese Guinea. The streak was 22 mm. long and 1 mm. wide, studded with a single series of circular pores, from each of which a single short hair arose. The gland itself, when extracted, measured about 27 mm. long, 10 mm. wide, and 5 mm. in vertical depth. In section, both longitudinal and transverse, it was pale externally, with its central third forming a dark core. Under slight pressure drops of clear fluid, like liquid gum tragacanth, could be squeezed from the pores. When rubbed between the fingers it became, as it dried, quite sticky, giving out a faintly aromatic odour like that of black-currant tea. Under hard pressure pale whitish-grey maggot-like threads could be expressed from the pores.

Inguinal glands were absent as in *G. macwelli*.

The feet were constructed as in the last-named species, with the marked difference that the pedal gland consisted of a simple narrow cylindrical tube not extending so far as the false hoofs and showing no sign of expanding between the bones into an enlarged laterally compressed dilatation.

Although superficially *G. macwelli* and *G. melanorheus* are so much alike that it has been suggested that they be regarded merely as subspecies, it appears to me that the difference in the structure of their pedal glands entitles the two to specific separation, at all events until further examination has shown that this character has not the value here claimed for it.

Text-fig. 93.



A. Median vertical section of hind foot of *Guevei aqua*

B. Do. of front foot of the same.

C. Do. of hind foot of *G. melanorheus*.

(All dried specimens.)

Genus CEPHALOPHUS H. Sm.

CEPHALOPHUS DORSALIS Gray. (The Bay Duiker.)

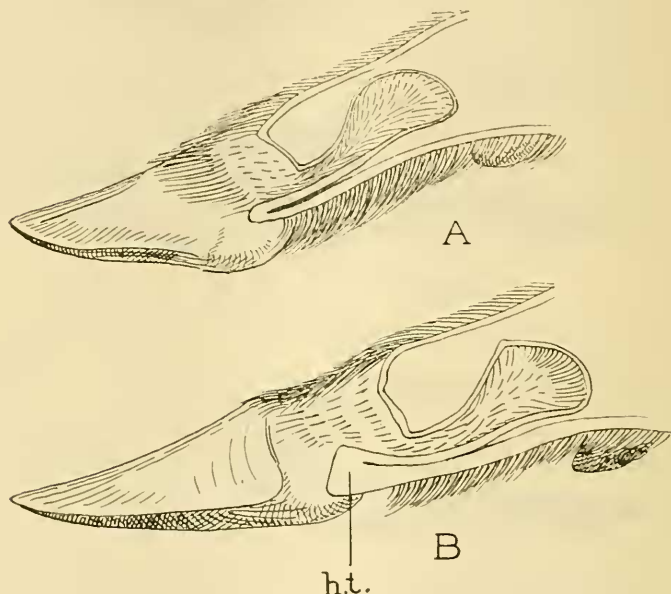
A single example from Sekondi presented by Capt. C. H. Armitage.

The preorbital streak was straight, 22 mm. long, 1 mm. wide, and studded with a single row of 14 pores, from which grey-coloured fluid could be pressed.

Inguinal glands were well developed and widely separated by a space of 42 mm. from the two mammæ of each side. There was only a single pair of these glands. Each consisted of a long sac very gradually expanding internally from the orifice, the walls of

the bottom third of the pocket being corrugated and ridged. The secretion was yellow and sticky. The structure of the feet was almost the same as in the species already described, except that the fold of integument forming the web at the heels was enormously thickened and horny, forming a very strong union between the two hoofs behind. Moreover, this interdigital depression was only scantily clothed with shortish hairs, the tips of which scarcely overlapped the margin of the nail of the hoofs, except

Text-fig. 94.



A. Median vertical section of foot ($\frac{1}{2}$ front or hind) of *Sylicapra grimmii*, subsp.?
 B. The same of hind foot of *Cephalophus nigrifrons*. ht., heel-tie.

(Both dried specimens.)

quite in front. The pedal gland itself was not dissected out, but its circular orifice was apparent. Apart from other features, *C. dorsalis* differs from the species of the *marcellii* group in possessing inguinal glands; and in this connection it may be noted that Owen records the presence of inguinal glands in *C. silvicultrix*, one of the larger species of the genus usually considered to be related to *C. dorsalis*.

CEPHALOPHUS NIGRIFRONS Gray. (The Black-fronted Duiker.)
 (Text-fig. 94, B.)

A female example of this species, kindly lent to me by Mr. Gerrard, agreed with *C. dorsalis* in possessing a pair

of inguinal glands consisting of deep subcylindrical pouches, with the orifices remote from the mammae. The interdigital cleft was scantily hairy and the heel-tie was very thick as in *C. dorsalis*; and the pedal gland on all four feet consisted of a long expanded sac with a small orifice, as in *G. macrilli* and in *S. coronatus*.

CEPHALOPHIUS SILVICULTRIX.

(The Yellow-backed Duiker.)

In two dried and flat skins from the Cameroons, kindly given to me by Rowland Ward, Ltd., I found the feet and pedal glands constructed as in *C. nigrifrons*. About the inguinal glands on these skins I can affirm nothing. Owen, however, says they were present in the species.

Genus SYLVICAPRA Ogilby.

SYLVICAPRA CORONATA Gray, 1842.

subsp. CAMPBELLIE Gray (?) 1843*.

Of specimens referred to this species, I have examined several from various parts of Nigeria, including two young males from Sokoto, presented by Major Searight, and one from Ibadan in the Yoruba country, presented by Mr. T. Christ.

In all of them the preorbital streak was lightly concave upwards, thus differing in shape from that of the Duikers of the *macrilli* group, and also, though in a lesser degree, from that of *C. dorsalis*. The streak was studded with a series of 15 or more pores, from which fluid secretion with a pleasant aromatic odour could be squeezed. Under continued pressure black coiling worm-like threads of a waxy consistency exuded.

A pair of inguinal glands consisting of wide but (in the young) shallow pits were present. They were much shallower than in *C. dorsalis*; but their orifices, as in that species, were situated a long way from the two mammae on each side, lying in fact just on the femoral side of the fold or crease between the inner surface of the thigh and the abdomen: and, as in *C. dorsalis*, the whole inguinal and mammary area of the abdomen was naked as far out as the glandular orifices. The secretion of the inguinal glands smelt like sour milk in two examples, but had an objectionable faecal odour in another.

The feet were constructed as in other species of this group.

* According to Gray (Cat. Rum. B. M. p. 23, 1872), *C. campbellie* was in 1872 represented in the British Museum by a single skin from West Africa, which he marked interrogatively as having been obtained at Sierra Leone. The skin agrees tolerably closely with the Nigerian examples that I have seen. I think, therefore, that Gray was probably correct in assigning his type to West Africa; and that it was an error to suppose that the name *campbellie* belongs to a Natal form of *Sylvicapra* (Lydekker, 'Game Animals of Africa,' p. 142, 1908). *S. coronata* Gray, from Senegambia, appears to me to be a paler form of the same species.

but the walls of the triangular interdigital depression leading to the gland were very sparsely clothed with quite short hairs, much fewer and shorter than in *C. dorsalis*. Only at the inferior margin of the side walls of the depression were there long hairs overlapping the proximal edge of the nail of the hoof. The gland itself consisted of a large laterally compressed sac, very much like that of *G. marwelli*, but with the narrowed portion much shorter and wider, and with no long hairs jutting from the orifice, the walls of the sac being clothed with very short sparsely set hairs, like those of the triangular depression. As in *G. marwelli*, the glandular tissue could be traced not only over the walls of the gland itself but from the commencement of the anterior web of the hoofs to that of the posterior web. There was, however, no secretion in the glands.

My observations on this species agree with those made on *S. grimmii* by Ogilby, who stated that both inguinal glands and pedal glands were present, the latter being small. Owen also found inguinal glands in *S. grimmii*.

In an odd foot of a *Sylvicapra* closely related to the typical *S. grimmii*, and given to me by Mr. Gerrard (text-fig. 94, A) I found pedal glands resembling in all essential points those of the legs of the examples identified above as *S. coronata*.

The features to be noticed in connection with the cutaneous glands of the Cephalophinae are the general constancy of the structure of the preorbital gland and of the feet and the minor differences presented by each. The preorbital gland is always large, oval, tough and india-rubbery in consistency, is situated farther forwards than in other Antelopes, and has no valvular invagination of the skin connected with it as in Gazelles, Sheep, Dik-Diks, and others. Instead of this it communicates with the exterior by means of a series of setiferous pores placed on a narrow strip of bare integument. It differs, in fact, from that of all other Ruminants.

The structure of the feet, too, is very uniform. They do not, however, differ materially from those of *Madoqua*, as illustrated by *M. phillipsii*, nor from genera of Neotraginae that I have examined, namely *Ourebia* and *Raphicerus*. Only in one little point is there, within my experience, a constant difference. Whereas in the Madoquinae and Neotraginae the web joining the heels is covered continuously with long hairs, in the Cephalophinae the back of this area of integument is always naked for a longer or shorter distance.

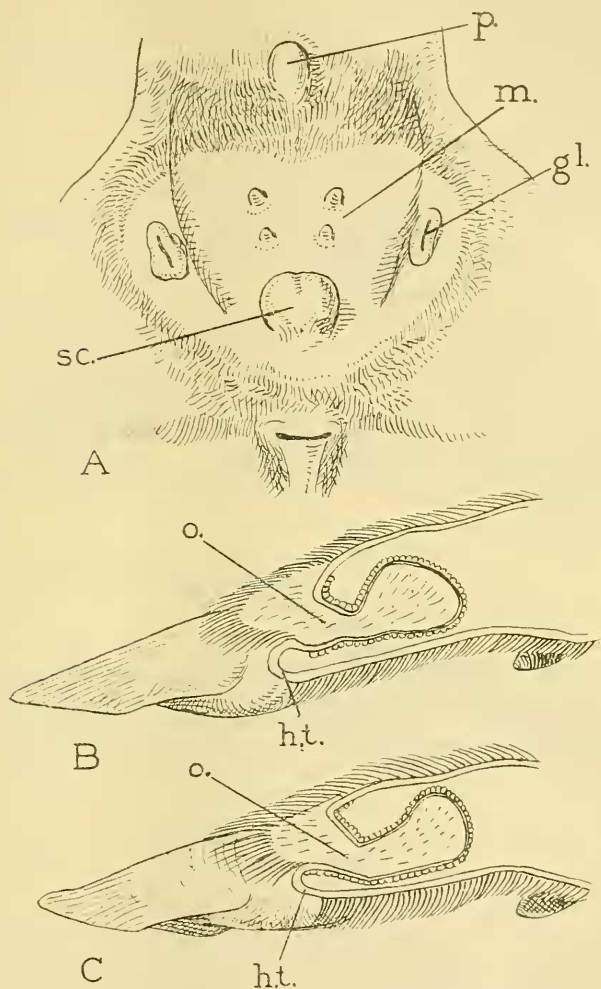
Another peculiar feature of the Cephalophinae is the wide separation of the inguinal glands, when present, from the mammae. In this particular, however, they resemble some Tragelaphinae and *Pantholops*.

In my opinion the absence of the inguinal glands* in the forms

* This difference, as well as others, between *melanorheus* and *dorsalis* was noted on the same material by Mr. F. E. Beddard (P. Z. S. 1909, i. p. 181).

above identified as *maxwelli*, *aequatorialis*, and *melanorheus*, points to their generic separation from those referred to *dorsalis*,

Text-fig. 95.

*Sylvicapra coronata*.

- A. Inguinal region of male: *p.*, penis; *m.*, mammae; *gl.*, orifice of gland;
sc., scrotum.
 B. Median vertical section of front foot.
 C. The same of hind foot.

o., orifice of gland; *h.t.*, heel-tic.

(All fresh specimens.)

nigrifrons, and *coronata*, of which *abyssinica** is, I think, a subspecies.

It is, moreover, well known that the group exemplified by *coronata* differs from that exemplified by *dorsalis* in the markedly more upright inclination of the horns. If generic importance be attached to that character, a proceeding desirable on the grounds of the unwieldiness of the genus *Cephalophus* as at present recognised, the genus can be split at all events into three genera which may be distinguished as follows:—

- | | |
|--|----------------------|
| <i>a</i> . Inguinal glands absent | <i>Guerzi</i> . |
| <i>a'</i> . Inguinal glands present, consisting of a pair of deep pouches, the orifices of which are remote from the mammae. | |
| <i>b</i> . Horns inclined backwards in the plane of the face; ears short | <i>Cephalophus</i> . |
| <i>b'</i> . Horns inclined upwards and backwards, forming an obtuse angle with the plane of the face; ears long | <i>Sylvicapra</i> . |

The type of the genus *Guerzi*, as selected by Messrs. Selater and Thomas, is *maxwelli*, with which *aequatorialis* and *melanorheus* must be associated. The type of *Cephalophus* is said to be *silvicultrix*, a species in which Owen affirms the existence of inguinal glands. As defined above, the genus also contains *dorsalis* and *nigrifrons*. The type of *Sylvicapra* is *mergens*, but *grimmii* appears to be the oldest name given to the species.

For the characters of *Tetraceros*, usually referred to the Cephalophinae, see p. 921.

Subfamily MADOQUINÆ.

Genus MADOQUA Ogilby.

(Dik-diks.)

The available evidence suggests that the species of this genus possess preorbital and pedal glands, but are without inguinal glands. In the case of *M. saltiana*, both Owen and Ogilby are in agreement about the presence of preorbital and the absence of inguinal glands, and Ogilby adds that the pedal glands are also present.

MADOQUA PHILLIPSI Thomas. (Lort Phillips's Dik-dik.)

(Text-fig. 96.)

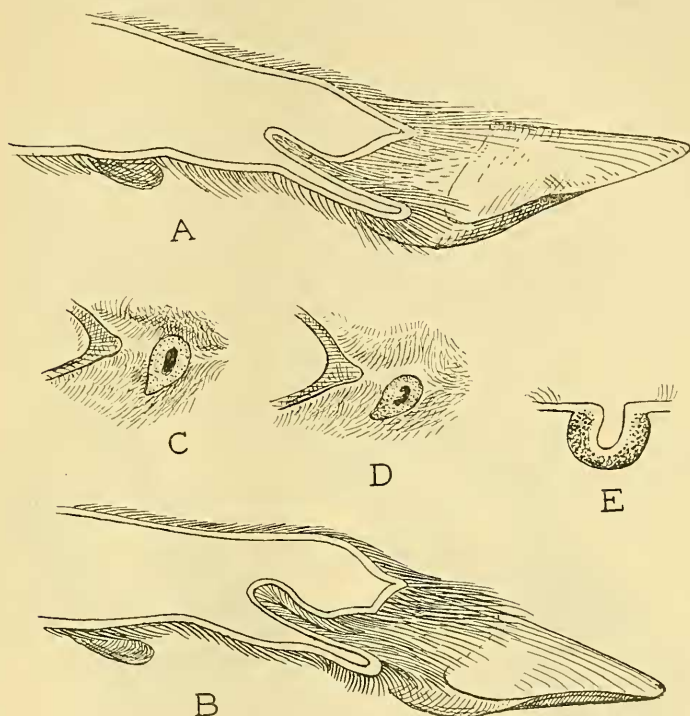
Of this species I have examined, in the fresh state, one example which agreed with the specimens of *M. saltiana* seen by Owen and Ogilby in having preorbital and pedal glands, but no inguinal glands. Mr. Beddard also noted the absence of inguinal glands (P. Z. S. 1909, i, p. 188).

The preorbital glands were small. The orifice was a small vertical crescentic slit, with its concavity looking backwards.

* I here adopt, without prejudice, Mr. R. C. Wroughton's opinion that *S. abyssinica* differs from the southern form *C. grimmii* in the shortness of its ears. It is quite immaterial to the work in hand whether *abyssinica* be specifically or subspecifically distinct from *grimmii*, since the close relationship between the two is admitted by everyone.

situated in the middle of a naked oval patch of skin just in front of the orbit. The orifice led into a shallow integumental pocket, dipping into the substance of the black underlying gland. Under pressure thickish black secretion could be squeezed from the orifice.

Text-fig. 96.

*Madoqua phillipsii*.

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Preorbital gland with orifice distended.
- D. Ditto ditto closed.
- E. Ditto in section.

The two halves of the feet were united in the middle line by two "webs," an anterior and a posterior, the posterior extending as far downwards as the heels and constituting the posterior wall of the interdigital space, the anterior being some little distance above the proximal margin of the hoofs, which were thus capable of much greater distension anteriorly than posteriorly. Beneath the anterior web, the integument receded obliquely backwards and upwards, and gradually passed into the anterior wall of a short subcylindrical tube running upwards

between the phalanges, the posterior wall of this tube being formed by the posterior web of integument. In longitudinal section the gland had the appearance of a narrow cylindrical tube opening by a wide orifice into the interdigital space. The tube and this space were alike lined with hair, which on the lower lip of the orifice formed a longish tuft to guide the secretion down between the heels of the hoofs. The posterior web was continuously hairy all along its back and inferior edge.

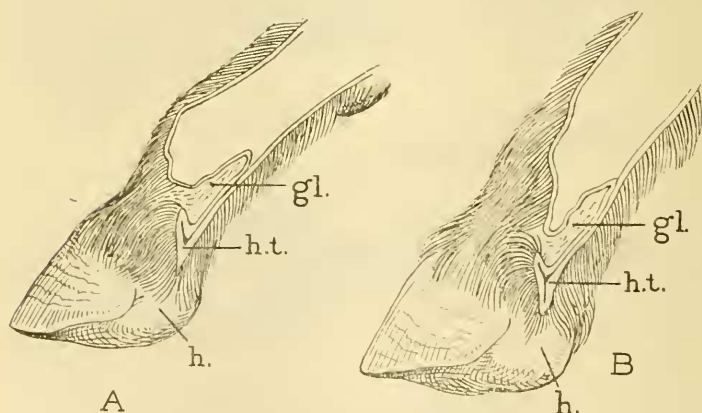
Genus *DORCOTRAGUS* Noack.

DORCOTRAGUS MEGALOTIS Menges. (The Beira.)

(Text-fig. 97.)

Of this rare and anomalous Antelope I have seen only the dried skins in the British Museum. Through the kindness of Mr. Oldfield Thomas I was enabled to examine the pedal glands of one of these; and their structure convinces me that *Dorcotragus* is allied to *Madoqua*, but adapted to a mountainous

Text-fig. 97.



Dorcotragus megalotis.

- A. Median vertical section of hind foot.
 B. The same of front foot on a slightly larger scale.
gl., gland; *h.t.*, heel-tie; *h.*, heel.

(Dried specimens.)

habitat. The feet have acquired a superficial resemblance to those of Goats and Sheep, owing to the shortness of the nail and the great development of the sole and heel of the hoofs, the latter forming large cushion-like pads. The strong integumental bridge joins the hoofs together just above the heels; and the anterior edge of this is raised so as to form an upstanding lower lip to the orifice of the gland. The latter is a depressed elongated

pouch, recalling that of *Madoqua phillipsii*, except that the orifice is much smaller in consequence of the ridge-like lower rim. This rim seems to be developed in connection with the vertical position of the feet when the animal stands, not only increasing the size and strength of the interdigital union, but serving to check the otherwise uninterrupted downward flow of the secretion from the gland by forming a barrier, above which it accumulates. The pocket of the gland is somewhat sparsely lined with short hairs; those on the upstanding lower rim of its orifice are longer, serving to conduct the secretion outwards, as in *Madoqua*. It is noticeable that in *Rhaphicerus campestris* and *Madoqua phillipsii* the entire interdigital integument is covered with hair, there being no naked space behind the heel-tie such as is seen in the species of *Cephalophinae* examined by me. The deep depression between the penultimate phalanges of the foot into which the gland opens resembles that of Sheep and Goats.

On the dry skin I can find no trace either of preorbital or inguinal glands, and there appears to be a single pair of teats.

Messrs. Sclater and Thomas, though apparently not without misgivings ('Book of Antelopes,' iii. pp. 1, 2, 1897), placed this Antelope in the subfamily Antilopinae, "near the Gazelles," and considered as "superficial" the "resemblance it bears to certain members of the subfamily Neotraginae." It appears to me, however, that its affinities, as attested by the horns, skull, muzzle, and coloration, not to mention the apparent absence of inguinal glands and the structure of the pedal glands, are more Madoquine than Gazelline.

Using the feet and preorbital gland as a basis, these two genera may be distinguished as follows:—

- | | |
|--|----------------------|
| a. Hoofs more or less elongate, with normal sole and heels; heel-tie formed by a simple fold of integument; a preorbital gland present..... | <i>Madoqua</i> . |
| a'. Hoofs short, with pad-like soles and heels; heel-tie forming a double fold, the anterior fold projecting as a ridge constituting a kind of lower lip to the orifice of the pedal gland; no pre-orbital gland | <i>Dorcotragus</i> . |

Subfamily NEOTRAGINÆ.

Genus RAPHICERUS H. Sm.

RAPHICERUS CAMPESTRIS Thunb. (= *Pediotragus tragulus*).

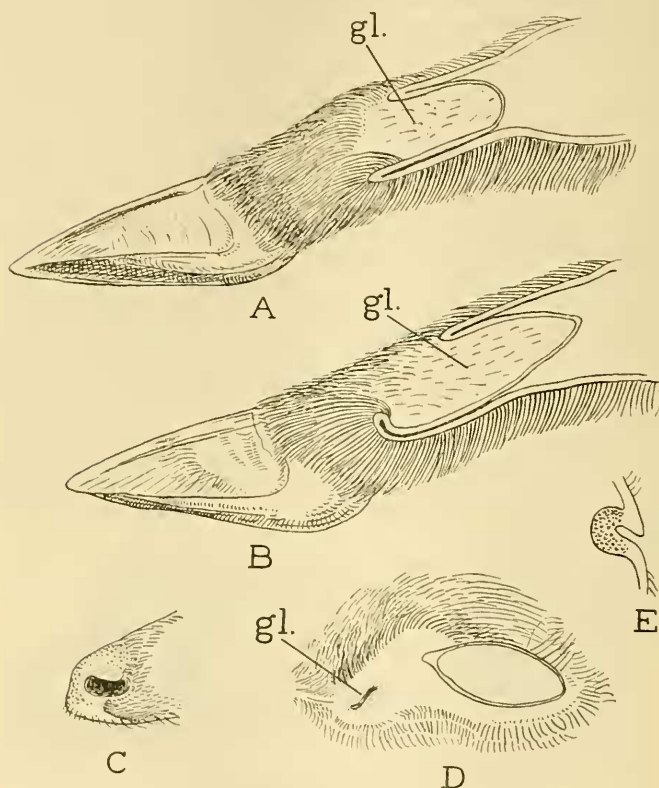
(The Steinbok.) (Text-fig. 98.)

The presence of preorbital and inguinal glands was recorded by Owen; and according to Max Weber, who cites the species under the names *Pediotragus tragulus* and *rufescens*, the preorbital glands are present in both sexes.

Of this species I have examined two old stuffed examples, which the Committee of the Bristol Museum and Art Gallery kindly permitted Mr. Herbert Bolton, F.R.S.E., F.Z.S., the Curator, to send to me.

Neither specimen showed any trace of inguinal glands. This, however, cannot be regarded as satisfactory evidence of their absence, since the skins were mounted and dried.

Text-fig. 98.

*Raphicerus campestris.*

- A. Median vertical section of hind foot: *gl.*, pedal gland.
- B. The same of front foot.
- C. Muzzle or rhinarium.
- D. Ocular region of female showing orifice of preorbital gland.
- E. Section of the same gland.

The preorbital glands were placed near the anterior edge of a large area of naked skin in front of the eye. The orifice formed a small oblique slit, with a slight sigmoid curvature. This led into a scantily hairy pocket, dipping into the gland, which, as in *Madoqua phillipsii*, formed a small, nearly black mass. The upper margin of the orifice formed a kind of lid over the pocket. The gland was larger in the male than in the female.

The pedal glands were well developed, but different from those of *Madoqua*. On both front and hind legs they consisted of large wide-mouthed deep pouches passing up between the antepenultimate phalanges of the feet, and opening some distance above the proximal margin of the hoofs. The anterior wall of each was formed by a closely folded web, and the posterior by an equally closely folded posterior web; but neither of these webs extended so far down the foot as in *Madoqua*, the posterior web of the hind foot not nearly reaching the heels, and extending only a little farther than in the *Tragulina*, and reaching only a little farther than the anterior web. This suggests that the heels, as well as the rest of the hoofs, are capable of very wide separation. On the front foot, on the contrary, the posterior web was longer, and reached almost to the heels, extending considerably lower than the anterior web. Its inferior extremity, moreover, was turned slightly forwards for a short distance, making a distinct ridge, something like that of *Dorcotragus*. Although the walls of the pocket were only scantily clothed with hair, the rest of the interdigital space was clothed with long hairs, and the edge of the posterior web forming the posterior lip of the pocket was furnished with long hairs projecting downwards, as in *Madoqua* and *Dorcotragus*. There were two pairs of teats.

RAPHICERUS sp.? or NESOTRAGUS sp.?

I am indebted to Mr. Gerrard for a front and a hind foot without supplementary hoofs, and therefore referable probably either to *Raphicerus* or *Nesotragus*. These are worth describing, because they are structurally nearly intermediate between the feet of *Raphicerus campestris* and of *Ourebia nigricaudata*.

In the hind foot the interdigital cleft was open in front throughout nearly the whole of its length, being only slightly overlapped above by a short angular fold of integument. Its posterior wall descended with a gradual curvature downwards, meeting the skin of the back of the pastern considerably nearer the heels than in *R. campestris*, and forming a strong thickened tie, which was turned slightly forwards.

The interdigital cleft on the front foot hardly differed from that of *Ourebia nigricaudata*, except that its upper extremity was overlapped to a greater extent, although not so much as in *R. campestris*, by the antero-superior integumental web.

Since the hind foot was of a more rusty tawny hue than the front foot, and measured half an inch more from the fetlock to the tip of the hoof, there can be very little doubt that it belonged to a different species or subspecies, possibly to a different genus, of Autelope. Considering the differences the two feet present from those of *R. campestris*, the evidence is, I think, in favour of their belonging to the genera *Neotragus* or *Nesotragus*, perhaps one to *moschatus* and the other to *livingstonianus*.

*Nototragus** *melanotis* Thunb. (the Grysbok) has, according to Owen, preorbital and inguinal glands. Max Weber, however, says that although the preorbital gland ("Thränengrube") is present in the male, in the female it is represented by a naked area of skin. This statement must be taken with reserve, in my opinion, since it does not appear to have been based upon fresh material (see under *Ourebia ourebi*). I have not examined material of this species.

Genus OUREBIA Laurill.

OUREBIA OUREBI Zimm. (= *scoparia* Schr.).

(The Cape Oribi.)

According to Owen, this species has large preorbital glands and inguinal pits. Max Weber, on the contrary, states that, although the male has a deep preorbital gland, this organ is apparently represented in the female by a naked spot in front of the eyes. This observation must, I think, have been made upon a mounted specimen, for I cannot reconcile it with the fact that in the female of *O. nigricaudata* described below, and in one of *O. montana*, now living in the Gardens, the preorbital gland is well developed and valvular.

OUREBIA NIGRICAUDATA Brooke.

(The Black-tailed Oribi.) (Text-figs. 99, 100.)

I have seen two young examples, male and female, of this species from Senegambia, presented by Sir George Denton. The preorbital gland was marked externally by a longish slit running downwards from a point close to the anterior angle of the eye. This was capable of considerable distension, and led into a simple pocket-like invagination dipping into a large, oval, black, glandular mass. Under pressure, the secretion, black and adhesive like lamp-black, could be squeezed from two areas marked by depressions, one near the middle, the other upon the upper corner of the gland. Each depression contained several pores, from which long coiling threads of the substance exuded. The gland and its orifice were relatively longer in the male than in the female.

The so-called glandular patch beneath the ear was rather scantily clothed with very short hairs. In section the skin was seen to be markedly thinner than that of the surrounding area, and showed no evidence of specially developed glands.

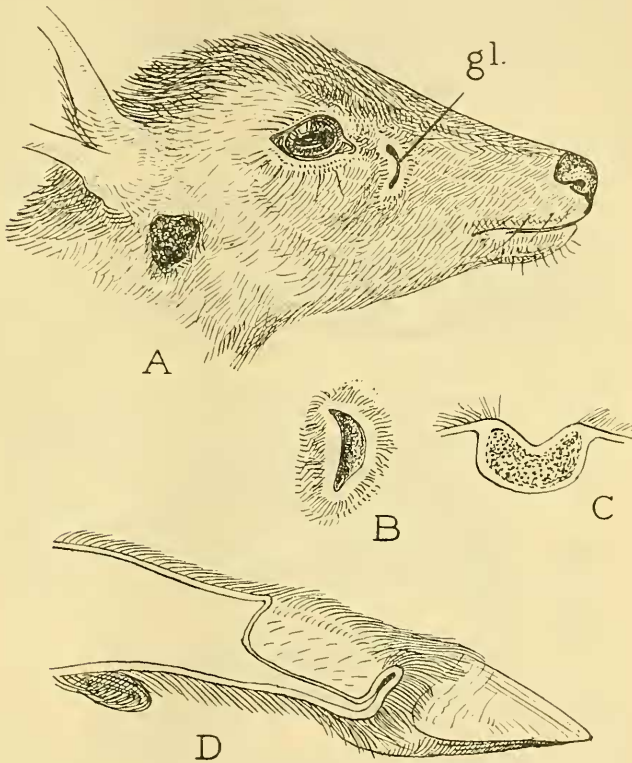
There were two pairs of teats.

The inguinal glands were represented in the female by a pair of

* This generic name was proposed by Thomas and Schwann for the Grysbok (Abstr. P. Z. S. No. 27, p. 10, 1906), because it differs from *Rhaphicercus* in possessing supplementary hoofs. Mr. Lydekker's statement, therefore, that the genus was based upon *R. campestris* (the Steinbok), which has no supplementary hoofs, is erroneous ('The Game Animals of Africa,' p. 181, 1908).

shallow depressions, each marked by a tuft of hair arranged in a whorl and situated in the ordinary position near the mammae. In the male, however, they were far back alongside the scrotum, a very unusual position. Each consisted of a short sac, with tumid orifice, whence a large tuft of hairs protruded.

Text-fig. 99

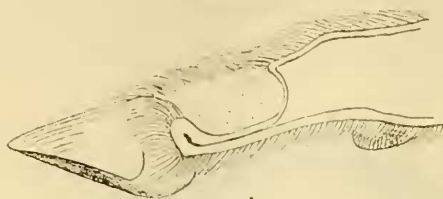
*Ourebia nigricaudata* ♀.

- A. Head to show orifice of preorbital gland (*gl.*) and nearly naked patch below ear.
- B. Preorbital gland with orifice distended.
- C. Section of preorbital gland.
- D. Median vertical section of front foot. (N.B. The hairs within the cleft are too long, coarse, and clearly defined.)

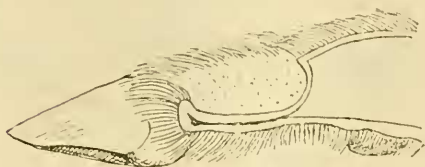
The tuft of hairs below the knees covered an area of thickened integument as in Gazelles. There were no special indications of glandular activity, however, beyond a certain amount of powdery scurf at the base of the long hairs.

The pedal glands, present on all four feet, were very like those of Gazelles, except that the fold of skin forming the heel-tie

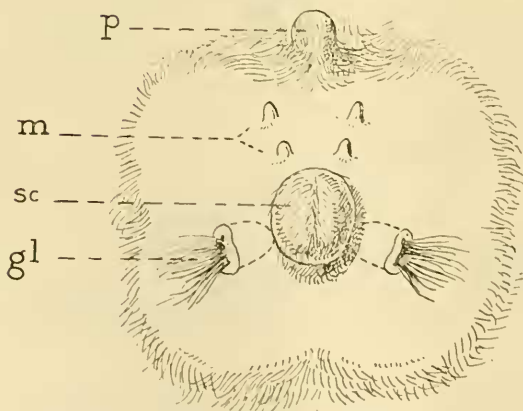
Text-fig. 100.



A



B



C

Ourebia nigricaudata ♂.

A. Median vertical section of front foot.

B. The same of hind foot.

C. Inguinal region: *p.*, penis; *m.*, mammae; *sc.*, scrotum; *gl.*, inguinal gland with tuft of hair protruding from the orifice.

extended less to the front, so that the cavity of the interdigital cleft was to a greater extent in communication with the space

between the hoofs. This was more marked in the male than in the female, and in the former sex the heel-tie was thinner and less produced in the hind than in the front leg. The walls of the glandular interdigital depression were scantily covered with short hairs; but the heel-tie itself was thickly clothed with long hairs, largely overlapping the base of the hoofs on their inner aspect. The chief difference between the feet of this species and those of *Raphicerus campestris* lies in the fact that the interdigital cleft is not overlapped above by a long integumental fold, and that the fold of skin along the back of the pastern extends right down to the heels, tying them together, and extends further forwards towards the anterior edge of the hoofs. From this arrangement it comes about that the hoofs of *Ourebia* are much less distensible than in *Raphicerus*; they are also shorter: the combination of these two features suggesting that *Ourebia* habitually frequents harder ground.

The structure of the feet in *Ourebia*, correlated with that of the preorbital glands and the presence of well-developed tufted carpal or knee glands and of a single pair of inguinal glands, is strongly suggestive of affinity between that genus and *Gazella*.

By the structure of the feet, *Ourebia* and *Raphicerus* may be distinguished as follows:—

- | | |
|---|--------------------|
| a. Orifice of glandular interdigital cleft much shorter than the cleft itself, which is partially overlapped in front and above by a longish integumental fold or web; posterior web of the pastern not reaching the heels, which can thus be widely separated..... | <i>Raphicerus.</i> |
| a'. Orifice of glandular interdigital cleft approximately as long as the cleft itself, which is not to any appreciable extent overlapped above and in front by an integumental fold; posterior web of the pastern reaching the heels, which are thus capable of being separated only to a very limited extent | <i>Ourebia.</i> |

Subfamily OREOTRAGINÆ.

Genus OREOTRAGUS H. SM.

OREOTRAGUS OREOTRAGUS Zimm. (The Klipspringer.)

(Text-fig. 101, A, B.)

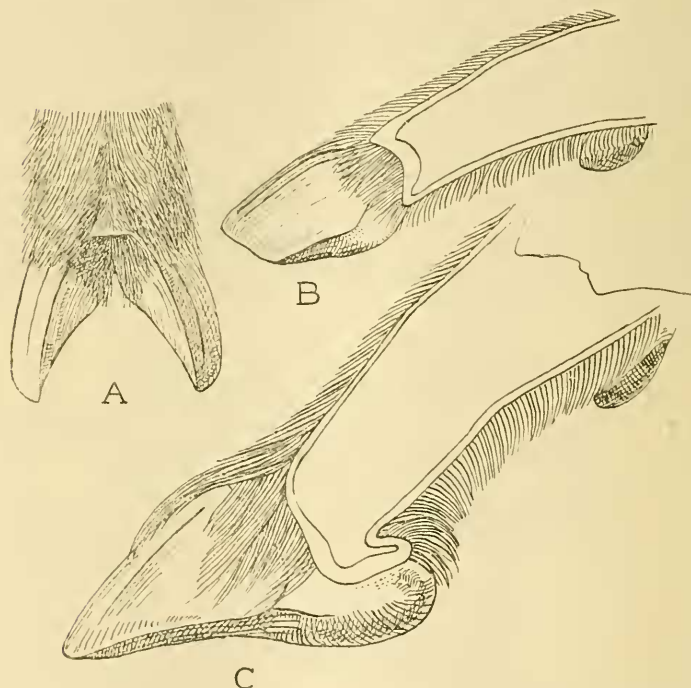
According to Owen, this species has preorbital glands but no inguinal pits. H. Smith, on the contrary, says that inguinal glands are present.

In a foot of this species, given to me by Rowland Ward, which had the bones of the pastern cut away from behind, but with the skin of the interungual area and of the front of the pastern entire, I could find no trace of pedal gland. The skin on the middle line of the pastern in front showed no sign of depression. Stopping short a little above the proximal margin of the hoof, it turned sharply backwards at right angles between the hoofs to

form the interungual web, which in section was shown to be thick and horny and to meet that of the back of the pastern just above the heels.

Thus the foot of this genus differs essentially from that of the genera of Neotraginæ above described, in that the integument of the back of the pastern is not folded back upon itself to form the posterior wall of an interdigital cleft or depression. But, as in

Text-fig. 101.



- A. Anterior view of pastern of *Oreotragus oreotragus* (? of front or hind foot) with hoofs distended.
B. Median vertical section of the same foot.
C. The same of front foot of *Pantholeps hodgsoni*.

the Neotraginæ, the interungual area is covered with long hairs from the front of the pastern to the back, there being merely a small triangular naked spot at the summit of the interungual web. In spite of the thickness and strength of this web, the hoofs can be widely separated and, as is well known, their points are very broad and truncated, the animal resting upon these truncated extremities instead of on the heels.

Subfamily ANTILOPINÆ.

Genus *GAZELLA* Licht. (Text-figs. 102, 103, 104, A-C.)

According to Owen, the following species of *Gazella* have large preorbital glands and inguinal pits:—*G. dorcas*, *subgutturosa*, *bennettii*, *arabica*, *sæmmeringii*, *mhor*, *ruficollis*, *rufifrons* (*kecella*)*. With these he contrasts *colus* and *gutturosa* as having small preorbital glands.

Ogilby states that this genus has distinct and movable preorbital glands, very large pedal and inguinal glands, and one pair of mammae.

Hodgson examined *G. dorcas* and *G. bennettii*. He correctly says of the former that it possesses distinct preorbital glands, large pedal glands on all four feet, and large and distinct inguinal glands. Of *G. bennettii*, on the contrary, he asserts that the preorbital glands are absent, and he consequently erected the genus *Tragops* for its reception. Blanford and others, however, say that these glands are present in *G. bennettii*, an observation quite in accord with my own.

Of the genus *Gazella* I have examined one or more specimens of the following species:—

G. bennettii. Several examples of both sexes, mostly from Persia.

G. subgutturosa. One male and one female from Meshed.

G. marica. Two males from Central Arabia.

G. muscatensis. Several specimens from South Arabia.

G. dorcas. An adult pair from Egypt.

G. pelzelni (?). One quite young female from Somaliland.

G. cuvieri. One old female from Morocco.

G. rufifrons. One young male from Senegal.

G. sæmmeringii. One skin of an adult male lent by Mr. E. Gerrard.

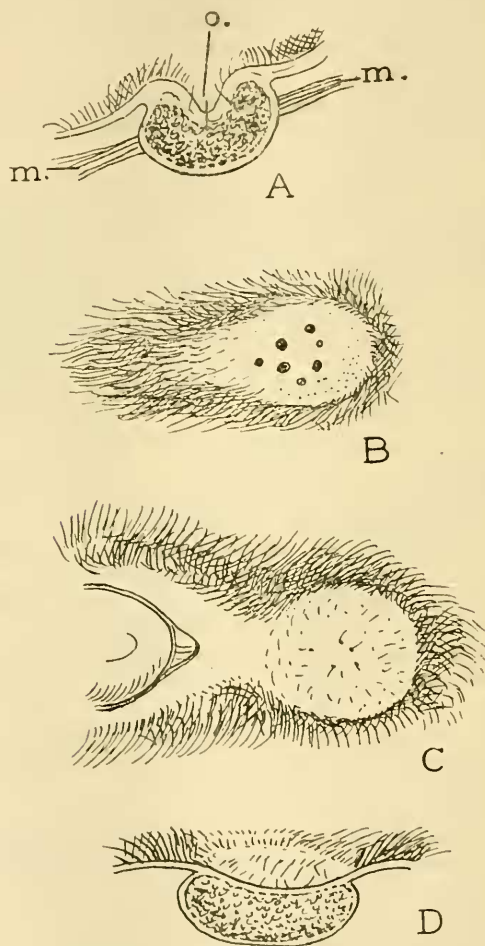
So constant in structure and occurrence are all the glands that a detailed description of them, as exhibited by each species, is unnecessary.

The preorbital gland is valvular. When closed it has the form of a vertical slit of black nearly hairless skin extending downwards from a point a little in front of the anterior corner of the eye. When opened to its fullest extent, it appears as a subcircular patch of skin, scantily beset with short hairs, and marked with a shallow central depression, which is, in reality, the bottom of the invaginated pocket. The gland itself, when extracted from the preorbital pit of the skull, is seen to consist of a black integumental thickening formed round the invagination. In the case of *G. dorcas* I found that the inner surface of the pocket had about seven large holes, from which, under pressure,

* I infer that *rufifrons* is the species cited by Owen under the name "*kecella*," because he gives Senegal as its locality.

secretion could be squeezed first in the form of black waxy threads, then as fluid drops, the waxy consistency being due, I expect, to the pores being blocked and inoperative for some little time before

Text-fig. 102.



- A. Section of preorbital gland of *Gazella dorcas*: o., orifice of gland
m., muscle.
B. Superficial view of the same gland flattened.
C. Superficial view of the flattened preorbital gland of *G. curieri* ♀.
D. The same gland in section.

death. Fluid drops could also be squeezed from the hair-pores studding the surface of the integument. The secretion contained

in the pocket itself is black and sticky. It may here be mentioned that Ogilby long ago (P. Z. S. 1836, p. 38) described the preorbital gland of a Gazelle as being furnished with six excretory ducts placed nearly in a circle and with one central duct, from the orifices of which there issued strings of a dense ceruminous matter.

The inguinal glands are always two in number, consisting of deeper or shallower pouches opening by larger or smaller orifices situated just externally to the mammae. The pouches dip into a mass of vascular tissue just above the mammae. They are usually about one inch deep and about as wide inside as deep or a little wider, the integument surrounding the orifice and the mamma being naked. In a male *G. subgutturosa* the orifice was nearly as large in diameter as the scrotum; in *G. dorcas* and *G. muscatensis* it was considerably smaller and the lumen of the pouch was correspondingly smaller in the two latter than in the former. The largest gland of all was found in the female of *G. cuvieri*, in which it was two inches deep and about twice as deep as wide, and as wide at the orifice as within.

The walls of the pocket were, in all cases, sparsely covered with short hairs, and the secretion was waxy and drier at the orifice than at the bottom of the pouch. It has a very strong odour. In *G. bennettii* and *subgutturosa* it is yellow in colour and smells exactly like the urine of the common House Mouse (*Mus musculus*); in *G. cuvieri* the colour is greenish yellow and the smell a mixture of mouse urine and flour-paste.

In a female of *G. dorcas* the inguinal gland secretion was pale green and resembled in scent a mixture of flour-paste and cheese; the pedal glands had a strong and decided, but peculiar and indescribable, smell; the secretion of the knee glands had a repulsive odour of dogs' dung, while that of the preorbital glands, although faint and quite indescribable, was not unpleasant. This specimen furnished an admirable instance of the fact below alluded to, that scents of totally different character may emanate from the glands of one and the same individual. This was further borne out by a specimen of *G. muscatensis*, in which the green secretion of the inguinal glands smelt exactly like cream-cheese, that of the knee gland like a Domesticated Sheep, while the pedal glands had a faint and indescribable, but different odour from either.

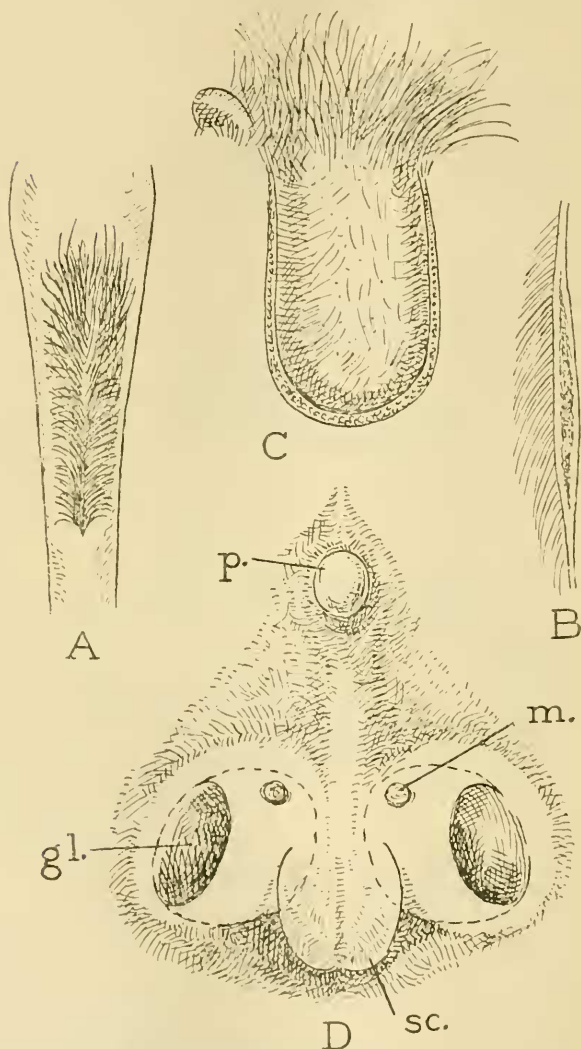
It may be noted in passing that the smell of the inguinal secretion in specimens of *G. bennettii* and *G. subgutturosa* from Persia is the same as that of *Ovis vignei* from the same country.

Although there is typically only a single pair of mammae in Gazelles, now and again there are two pairs, indicating, no doubt, the descent of these animals from quadrimammate ancestors. Similar atavism is sometimes seen in Sheep. When there are two pairs in Gazelles, the inguinal glands are connected with the posterior pair, showing that the anterior pair are supernumerary.

The pedal glands are well and equally developed on all four feet. When the hoofs are together, the orifice has the form of a narrow

slit dividing the hairs on the front of the pastern. When the hoofs are forcibly distended, it appears as a triangular cleft, pointed

Text-fig. 103.



- A. Superficial view of knee gland of *Gazella dorcas*.
 B. Longitudinal section of the same.
 C. Transverse section of inguinal gland of *G. curieri* ♀.
 D. Inguinal region of *G. subgutturosa*: p., penis; m., mamma; sc., scrotum; gl., orifice of inguinal gland, its area beneath the skin shown by dotted line.

above and wide below, above the base of the hoofs. The summit of the cleft is arched over to a small extent by a slight web of integument, and the bottom of it is closed by a strong and deep web which passes forwards from the heels of the hoofs to a point nearly on a level with their proximal edge in front. This web firmly ties the hoofs together, so that, in a living animal standing naturally, they never splay apart like those of Sheep and Goats, although when it rears up against anything the front hoofs often spread to a considerable extent. The skin forming the interungual web is folded sharply upon itself in front and passes back to the heels; its inner layer thence passes upwards only a little in front of the skin of the back of the pastern, then curves forwards about on a level with the joint between the penultimate and antepenultimate phalanges to meet the skin of the front of the pastern in the small web described above, thus forming the bottom, back, and top of the long interdigital cleft, the orifice of which is almost as long as the cleft itself. The walls of the cleft are only sparsely covered with short hairs; and I have never detected any signs of secretion either on them or on the longer hairs fringing the edges of the orifice or on the tufts of still longer hairs overhanging the proximal portion of the hoofs in front.

The interungual web is continuously hairy from front to back, though the hairs often become somewhat thinner towards the heels. The latter are well developed, and the hoofs are never long, though in these two particulars they are not specialised to the same extent as in Goats and Sheep, which stand rather more upright than Gazelles.

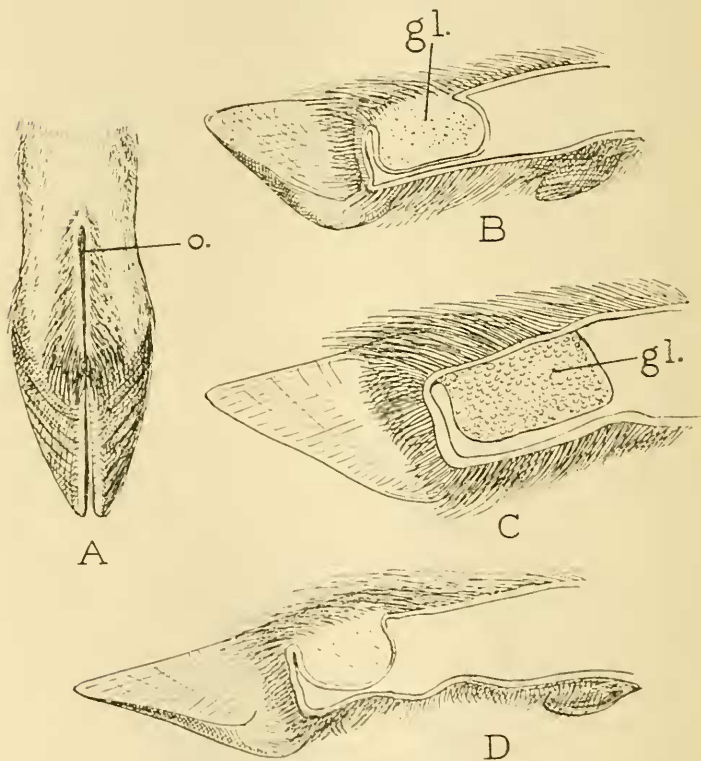
Dr. Murie long ago pointed out that the knee-tufts of *Saiga* are glandular. Mr. Lydekker made the same suggestion with regard to Gazelles ('Field,' March 14, 1908). This suggestion proves to be correct. The hairs are directed downwards, those on each side of the middle line usually crossing at the tips, somewhat as in the metatarsal gland of the Impala (*Epyceros melampus*). The underlying skin is much thicker than that of the rest of the leg; but the thickening, accompanied by increase in size of the sebaceous glands, is not abrupt but gradual, thinning away into the normal skin all round the circumference of the area. The hairs covering the latter hold a quantity of scurfy secretion.

As a general rule, the knee-glands are covered with long hairs forming a continuous pad and not showing, when undisturbed, any central longitudinal line; but in three examples of *G. dama ruficollis*, now living in the Gardens, the hairs are quite short and their inwardly directed tips do not meet in the middle line, so that the median gutter is plainly visible.

According to Hodgson the Tibetan species of Gazelle known as *picticaudata* has no preorbital or inguinal glands and has small pedal glands on all four feet. If his account be trustworthy, the species differs from all the true Gazelles I have examined in the absence of the preorbital and inguinal glands, not to mention the

seemingly smaller size of the pedal glands. Hodgson erected the genus *Procapra* for *picticaudata*; and, in view of the constancy in occurrence and development of the cutaneous glands in the species of *Gazella* I have examined, I am disposed to think that *Procapra* should be admitted as a valid genus, comprising probably, in addition to *picticaudata*, *gutturosa* and *przewalskii*. I do not know whether these three species are in actual agreement as regards cutaneous glands; but they at least differ from all the southern species of *Gazelles* in the shortness of the tail.

Text-fig. 104.



- A. Hind foot of *Gazella subgutturosa* showing slit-like orifice of pedal gland (o).
 B. Median vertical section of front foot of *G. lemmetii*: gl., glandular cleft.
 C. Foot of *G. curvieri* dissected to show the gland in situ.
 D. Median vertical section of foot of *Antilocapra marsupialis*.

The validity of *Procapra* was discussed by Messrs. Selater and Thomas ('Book of Antelopes,' iii. p. 73), and the claims of the genus to recognition were dismissed on the grounds that three of the characters in which the above-mentioned species agree (namely,

the absence of knee-tufts, of preorbital glands, and of horns in the female) are not absolutely distinctive of the group; *G. subgutturosa*, for instance, has the female hornless and "several species besides [the three in question] are without knee-brushes, while the antorbital fossæ in others are so shallow as to be practically non-existent." In accordance, however, with the modern more restricted application of generic names, it may be doubted whether these reasons will be regarded as invalidating *Procapra* from recognition, especially as the shortness of the tail seems to be an absolutely distinctive feature of the three above-mentioned species, as compared with Gazelles proper.

Pallas, according to Gray*, says that the male of *G. gutturosa* has a follicle, like the musk-bag of *Moschus*, in front of the prepuce. Still more interesting is the record by Hodgson of the presence of a large sinus behind the horns in *picticaudata*. This probably represents the postcornual gland of *Rupicapra*. Indeed, four of the characters cited by Hodgson as diagnostic of *Procapra*, namely, the absence of preorbital glands and of inguinal glands, the presence of small pedal glands, as compared with those of *Gazella*, on all four feet, and of a postcornual sinus, apply equally well to *Rupicapra*; and it may be that in *P. picticaudata* we have the link between *Rupicapra* and *Gazella*. Possibly also the organisation of *Procapra* may throw some light upon the true position of *Saiga* and *Pantholops*.

Genus ANTIDORCAS Sund.

ANTIDORCAS MARSUPIALIS Zimm. (= *euchore*).

(The Springbuck.) (Text-fig. 104, D.)

According to Owen, this species, which he appears to quote twice, under the names *Antilope euchore* and *pygarga*, has large preorbital glands and inguinal glands.

No information as to the glands is contained either in Scater and Thomas's 'Book of Antelopes,' or in W. L. Scater's volume on 'The Mammals of S. Africa,' or in Rowland Ward's 'Great and Small Game of Africa.'

I have examined three examples of this species, two males and a female. The preorbital glands resemble those of the Gazelles described above, except that the gland itself is pale yellow instead of black in colour. When everted and squeezed, the gland yields a clear fluid.

In spite of what Owen says, there is no trace of inguinal glands.

Pedal glands are present on all four feet and so closely resemble those of Gazelles as to need no redescription.

There are no knee glands, the knee-tufts being absent, as has already been recorded by previous describers.

* Cat. Rum. Mamm. in B. M. p. 37, 1872.

To compensate, as it were, for the absence of inguinal and knee glands, the Springbuck has an immense dorsal gland, the skin underlying the well-known white dorsal shield having highly developed sebaceous glands secreting a yellow sticky substance which stains the bases of the white hairs yellow or forms a scurfy kind of powder about their roots. No such substance is found upon the hairs of the rest of the back; and the skin of the area in question has a markedly fatty appearance when stripped, its colour differentiating it at once from that of the shoulders and sides of the body. Mr. F. E. Beddard, F.R.S., long ago noticed the glandular nature of this patch and drew my attention to it.

Genus ANTILOPE Pall.

ANTILOPE CERVICAPRA Pall. (The Indian Blackbuck).

(Text-fig. 105, A-C.)

The large size of the preorbital gland in this species has attracted the attention of zoologists from early times. The presence of inguinal glands was recorded by Owen in 1836 and independently in the same year by Ogilby, who stated at the same time that there are large pedal glands and only one pair of mammae. These observations were repeated by Hodgson and have been copied by recent systematic authors.

Through Mr. Herbert Bolton, F.R.S.E., F.Z.S., I am indebted to the Committee of the Bristol Museum for the stuffed skin of a male of this species, and Mr. Gerrard kindly supplied me with another.

Mr. Gerrard's specimen had the preorbital glands intact and by cutting them I was able to see that they differed in no essential particulars from those of Gazelles, except that they were very much larger, the infolding forming a long deep hair-lined space, and the glandular portion being very thick and pale in colour. The structure and general features of this organ have already been described by Bennett, Owen, and others.

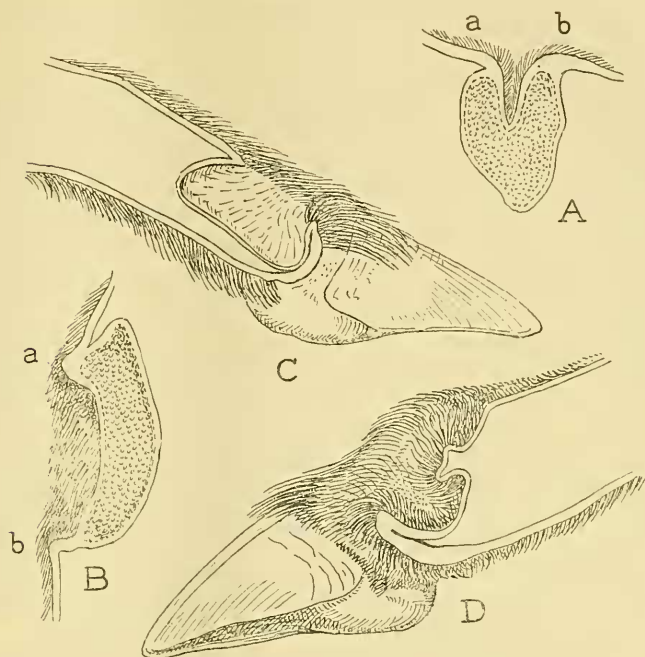
The orifices of the inguinal glands were clearly shown opening close to the mammae, of which there was a single pair.

The pedal glands were present in all four feet and were very like those of Gazelles. The walls of the interdigital cleft were furnished with longer hairs; the interungual integument was much thicker and more horny, forming a stronger tie between the hoofs; its anterior extremity was slightly recurved and furnished with a somewhat radiating tuft of hairs, the longest of which overhung the proximal edge of the hoof in front, while between this tuft and the heel-tie the skin was naked. There was no naked horny pad on the knees: but the knee gland was developed as in Gazelles, the roots of the long hairs being packed with scurf-like secretion.

The number, position, and structure of the cutaneous glands show close relationship between the genera *Antilope* and *Gazella*,

the only difference I can find between the two being the thickness, smoothness, and curvature of the interungual integument.

Text-fig. 105.



- A. Transverse section of preorbital gland of *Antelope cervicapra* ♂ :
 a, skin extending towards the eye; b, towards the nose.
 B. Vertical or longitudinal section of the same gland : a, upper, b, lower extremity.
 C. Median vertical section of front foot of *Antelope cervicapra*.
 D. The same of hind foot of *Lithocranius walleri*. (The fold in the integument of the wall of the gland probably absent in fresh specimen.)

In a living male specimen of this species the secretion of the inguinal glands smells exactly like flour-paste and might be described as starchy. The secretion of the preorbital gland is peculiar and indescribable. I cannot agree, however, with Bennett that the odour is urinous*.

* It is not, I believe, generally known to naturalists and sportsmen, though the fact is perhaps familiar to some who have paid attention to animals in captivity, that the adult male of this species undergoes a marked seasonal change of colour. During the summer months, that is to say, from about May to August, the colour, except of the face, is like that of females and young males, namely fawny. In the latter part of August or thereabouts, the coat begins to darken and gradually but rapidly assumes the dark hue whence the trivial name of the species "Blackbuck" has been derived. At or about the beginning of May the opposite change rapidly

GENUS *LITHOCRANIUS* Kohl.*LITHOCRANIUS WALLERI* Brooke.

(The Gerenook or Waller's Gazelle.) (Text-fig. 105, D, p. 895.)

No fresh material of this species has been available for examination.

Elliot describes the preorbital gland as a "conspicuous prominence with a central aperture, from which exudes a black secretion that stains everything it touches in the same way that ink does"*. Judging from this description the gland is better developed than in Gazelles, but the colour of the secretion appears to be the same.

On a fore and a hind foot kindly lent to me by Mr. Edward Gerrard I have found well-developed pedal glands, each consisting of a large saccular invagination on the front of the pastern. The orifice is as large as in Gazelles, and extends up the pastern as far as the joint between the penultimate and the antepenultimate phalanges. The inferior edge of the orifice is formed as in Gazelles by the interungual web, which, however, differs from that of Gazelles in passing only halfway along the space between the heels and the anterior proximal margin of the hoof. It is also much thicker and more horny than in Gazelles; but, as in the latter, is folded upon itself to form in the same way the back and upper wall of the glandular interdigital cleft. In the specimen examined, this wall was thrown into folds, suggesting a sac too voluminous for the space containing it. The walls of the gland were clothed with longish hairs, all projecting forwards or downwards towards the margins of the orifice, a downwardly directed fringe of hairs clothing the edge of the interungual web.

The entire pastern is clothed with very short close-set hair, with a small black tuft over the proximal end of the hoof in front; a felting of thick close-set hair clothes the integument on the inner surface of the hoof above the proximal margin of the nail and of the heels.

The hoofs are longer than in Gazelles, and capable of greater distension, on account of the web being shorter and situated somewhat higher above the hoofs.

Although the pedal glands of this genus are more like those

takes place, the first sign of it being a gradual lightening along the middle of the back. In August, when the blackening sets in, it appears first most pronouncedly upon the neck, legs, and fore quarters, and gradually spreads backwards.

For three consecutive years I have observed this in a specimen in our Gardens. I do not know what theory Indian sportsmen hold as to the disappearance of "Blackbucks" from the herds during the months they are in "eclipse" pelage, to borrow an ornithological expression. But, since most of them, I imagine, believe all tawny individuals to be does or young bucks, they must suppose, I conceive, that the adult bucks have separated themselves from their companions, an inference clearly not justified by the facts.

* 'Great and Small Game of Africa,' p. 371, 1899 (Rowland Ward).

of the Gazelles above described than they are like the glands of any other Antelope, they present well-marked differences from them.

There was a well-developed knee-pad of black and reddish hairs much longer than those of the surrounding skin and stuck together with plentiful dry secretion.

On skins of this genus in the British Museum I found two pairs of teats, but no evidence of inguinal glands.

As attested by other characters, this genus is an aberrant type most nearly allied to *Gazella*; but in the structure of the feet it seems to be less closely related to *Gazella* than is *Antelope* or *Antidorcas*. I do not feel sure, however, that the shape of the upper wall of the interdigital cleft in the example described and figured was not due to mutilation, since the skin of the pastern had been cut away at the back, perhaps thus loosening the connective tissue which normally holds the invaginated sac in place. It is very desirable that fresh examples of this species be examined.

Excluding *Procapra*, which I have not seen, the genera here referred to the Antilopinae may be distinguished as follows by the structure of the feet and by their cutaneous glands:—

- | | |
|--|-----------------------|
| a. An immense dorsal gland extending from the middle of the back to the rump, feet, and preorbital gland approximately as in <i>Gazella</i> , but no inguinal glands | <i>Antidorcas</i> . |
| a'. No dorsal gland. | |
| b. Feet with the folded interungual web extending only a little more than halfway between the heels and the proximal edge of the hoof in front; no inguinal glands; two pairs of mammae..... | <i>Lithocranius</i> . |
| b'. The folded interungual integument extending forwards nearly to the proximal margin of the hoof in front; a pair of inguinal glands; normally a single pair of mammae. | |
| c. Interungual integument thinner, hairy, the interdigital cleft practically naked | <i>Gazella</i> . |
| c'. Interungual web smooth; interdigital cleft more hairy... | <i>Antelope</i> . |

In addition to the four genera just described, the Antilopinae, according to accepted views, comprises the genera *Dorcotragus*, *Ammodorcas*, *Pantholops*, *Saiga*, and *Epyceros*. I do not, however, think these can be included in the subfamily without unwarrantably upsetting its homogeneity. Kinship is possible between *Ammodorcas* and *Epyceros* on the one hand and between *Saiga* and *Pantholops* on the other, but it does not appear to me that the two latter have any close relationship with the two former; it is indeed very far from obvious why the genera should be associated in the pairs suggested. Pending the demonstration of relationship such as would justify such a course, I propose to relegate *Pantholops*, *Saiga*, and *Epyceros* each to its own subfamily and to leave *Ammodorcas* for the present unplaced. In the following pages *Ammodorcas* will be found near the Cervicaprinae (p. 917). It may be added that these four genera differ widely in the structure of the feet from those here restricted to the Antilopinae.

Subfamily SAIGINÆ.

Genus SAIGA Gray.

SAIGA TARTARICA Linn. (The Saiga.)

According to Dr. Murie (P. Z. S. 1870, p. 500) this animal has a pair of small preorbital glandular pits; a pair of carpal or knee glands; a pair of shallow inguinal pouches in one specimen examined, but not in another, a younger example, although the secretory area was very evident; and pedal glands in all four feet. These are described as "about $1\frac{1}{2}$ inch in depth and opening by a narrow constricted aperture" at the "front and upper part" of the foot. Although on p. 502 of this memoir Dr. Murie remarks that these glands "hardly form satisfactory grounds for basing affinity upon," it is nevertheless quite clear from his description of the pedal glands that they are much more like those of a Sheep than of a Gazelle or Black-buck. The description is not sufficiently detailed to permit the conclusion that the pedal glands exactly resemble those of *Ovis*; but it is quite certain that with their narrow constricted orifice they bear no similarity to the long interdigital cleft of *Gazella* or *Antelope*. Their structure, in fact, bears out Dr. Murie's opinion that the Saiga may be regarded as an Antelopine Sheep.

In any case, it seems evident that the genus is an isolated one. I think, therefore, that it should form, provisionally at all events, the type of a special subfamily.

Subfamily PANTHOLOPINÆ.

Genus PANTHOLOPS Hodgk.

PANTHOLOPS HODGSONI Abel. (The Chiru.)

(Text-fig. 101, C, p. 886.)

In 1836 Hodgson (P. Z. S. 1836, p. 39) described the inguinal glands as "exceedingly large sacs which hang by a long narrow neck from the groin." He re-affirmed the same fact in other words in his paper in 1847, where he adds that preorbital glands are absent, but the pedal glands are present and large on all four feet. Blanford and Lydekker repeat his observations, without alluding to the pendent inguinal glands, while the latter supplements his account with Kinloch's observation that these glands penetrate a considerable distance into the body.

Hodgson's statement as to the pendulous nature of the inguinal glands is puzzling. It is hardly likely that they can be voluntarily eversible and retractile, and I can only suppose that he saw them hanging as loose sacs on a stripped skin.

The only material of this species I have been able to examine fully was a mounted head and two feet, fore and hind, of a male specimen, for which my best thanks are due to Mr. Edward

Gerrard, and a single foot shown by its colour to be that of a female, which was kindly given to me by Messrs. Rowland Ward, Ltd.

The head enabled me to confirm Hodgson's statement as to the absence of the preorbital gland, and the feet to refute his statement as to the presence of the pedal glands—they are absent. The integument along the middle line of the pastern forms a very shallow depression. Near the proximal end of the hoof in front it turns backwards at a rounded angle and runs almost parallel to the inner proximal margin of the nail to the heels, joining them together throughout their length. The posterior portion of the heels is well developed and the skin which unites them behind is folded sharply upon itself for a short distance, then turns up to be continuous with the skin of the back of the pastern. The back of the pastern and the fold in question are thickly hairy, and the interungual integument or web is covered with long hairs as far down as the point where the heel-tie begins. These hairs are especially long at the base of the hoof in front, and overhang the anterior edge of the nail nearly to its tip. Thus the integumental web which ties the hoofs together is as deep and strong as in Cattle (*Bos*) or Elands (*Taurotragus*), and the feet are quite different from those of typical Gazelles, to which *Pantholops* is usually held to be closely related; and the hoofs clearly have nothing like the power of extension seen in the feet of Sheep and Goats.

According to Hodgson, there is only a single pair of mammae, and I only succeeded in finding one pair in a dried skin of a male in the British Museum. I noticed in this skin that the orifice of the inguinal gland on each side lies some four or five inches away from the teat. On one side the gland was loose or pendent, as Hodgson described it; but on the other it was adherent and directed inwards from the orifice as a slightly expanding tube, its inner extremity lying close to the teat. This, no doubt, is its natural position, judging from the direction of the gland in other Bovidae that possess it.

In 1872 Gray recognised the peculiarities of this genus by placing it in a special family, *Pantholopidae*.

Saiga is commonly held to be related to *Pantholops*, perhaps correctly; but the relationship is not close. Apart from the well-known differences between them in the structure of the skull and nose, they may be distinguished as follows:—

- | | |
|---|---------------------------|
| <p><i>a.</i> Pedal glands, apparently ovine, on all four feet; preorbital glands present; inguinal glands small and close to the mammae, of which there are two pairs</p> | <p><i>Saiga.</i></p> |
| <p><i>a'.</i> No trace of pedal glands; no preorbital glands; inguinal glands very large and deep, with orifice remote from the mammae, of which there is a single pair</p> | <p><i>Pantholops.</i></p> |

In the characters here used, however, the two genera do not differ from each other much more than *Ovis* differs from *Pseudois* or *Capra*.

Subfamily BUBALINÆ.

(Hartebeests and Gnu.)

Of this group Owen records the presence of preorbital glands and the absence of inguinal glands in the following species:—*Damaliscus lunatus*, *Bubalis boselaphus* (= *Antilope babalis*), *B. caama*, *Gorgon taurinus*, and *Connochates gnu*.

Ogilby, who examined *Bubalis boselaphus*, which he quotes as *B. mauretanicus*, confirms Owen's statement regarding the above-given particulars, adding that the pedal glands are large and that there is a single pair of mammae.

Recent systematic writers agree with Ogilby as to the number of mammae; but in spite of his use of the epithets "*exigui, distincti*" in describing the preorbital glands, these are quite commonly, but erroneously, stated to be small.

Of Hartebeests belonging to the genus *Bubalis* I have seen no complete material, and have been compelled to rely upon soaked feet and masks usually with the skin only of the preorbital gland retained. Of the White-tailed Gnu (*Connochates gnu*) I have seen two freshly dead specimens. I have, however, seen living examples of the two species of Gnu (*G. taurinus*, *G. gnu*) and of two species of *Damaliscus* (*D. pygarga* and *D. albifrons*, the Bontebok and Blesbok respectively).

Genus BUBALIS Frisch.

BUBALIS CAAMA F. Cuv. (Text-fig. 106.)

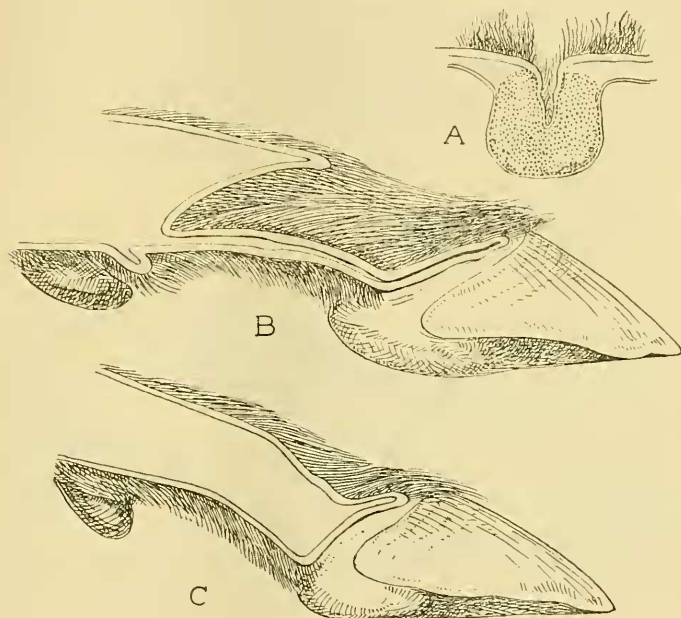
I am indebted to Mr. E. Gerrard for a mask, containing entire preorbital glands, and front and hind feet of this species.

The preorbital glands were covered with hairs which in the individual examined had a thickened appearance, owing to the coating of brown earthy-looking secretion which covered them individually. The centre of the area was marked by a distinct orifice leading into a narrow duct about half an inch long and lined with short hair. This duct penetrated about halfway into the large gland which was about as large as a walnut.

Pedal glands were present only on the fore feet, or if present on the hind feet they attained only a comparatively slight degree of development. On the fore feet they very closely resembled those of Gazelles, consisting of a very large interdigital cavity opening by a long orifice on the anterior aspect of the pastern and extending upwards from the proximal margin of the hoof in front. As in Gazelles the two hoofs were united by a deep interungual web, which extended from the heels to the proximal margin of the hoof in front, then folded sharply over and was continued backwards along its course nearly as far up as the false hoofs, where it turned obliquely forwards and downwards, meeting the skin of the front of the pastern at an acute angle to

form the anterior web joining the two halves of the pastern together in front. Although essentially of the same nature as in Gazelles this gland differed in one or two points. For instance, the height or length of the cavity along the back of the pastern was considerably greater than the length of the orifice, owing to the cavity being continued farther up the pastern than the edge of the anterior upper web. In the second place, the walls of the cavity were clothed with long blackish hairs which projected from the orifice, forming only a small tuft over the proximal margin

Text-fig. 106.

*Bubalis caama.*

- A. Vertical median section of preorbital gland.
- B. The same of front foot.
- C. The same of hind foot.

of the hoof. Lastly, the interungual web was quite naked back to the heels, and instead of meeting the skin of the back of the pastern at right angles met it at an obtuse angle, the difference of inclination being obviously correlated with the less upright position of the foot when standing, the long hoofs of the Hartebeest being much less vertical than the short hoofs of the Gazelles.

In the hind foot there was only a shallow depression just above

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the hoofs, the skin of the interungual web being folded back for only a short distance, then inclining obliquely upwards, forming the back wall of the depression in question. This depression on the hind foot might be compared to the depression on the pastern of the Chamois, except that its walls were hairy instead of nearly smooth.

Of the genus *Bubalis* I have also examined the face-skin and part of the gland of *B. cokei* supplied to me by Rowland Ward, Ltd., and by Mr. E. Gerrard. In this species the pre-orbital gland has essentially the same structure as in *B. caama*.

The following species also have the gland clothed externally with a mat or tuft of hairs, namely, *B. major*, *tora*, *swagueli*, *lebrei*, and *jacksoni*. In *B. lichtensteini*, on the contrary, the glandular area is naked as in *Damaliscus*, the orifice in the dry skin being a small slit-like aperture leading into a duct. The hind foot of *B. lichtensteini* is like that of *B. caama*, having only a shallow depression on the front of the pastern. For the material of the species, enabling me to establish these data, I am indebted to Mr. E. Gerrard.

Genus DAMALISCUS Sel. & Thos.

DAMALISCUS KORRIGUM Ogilby. Subsp. *JIMELA* Matsch.

(Text-fig. 107.)

I am indebted to Mr. E. Gerrard for the opportunity of examining a complete skin of this Hartebeest.

The preorbital gland itself was cut away, but the orifice was represented by a short elongated aperture in the middle of a bare patch of skin in front of the eye.

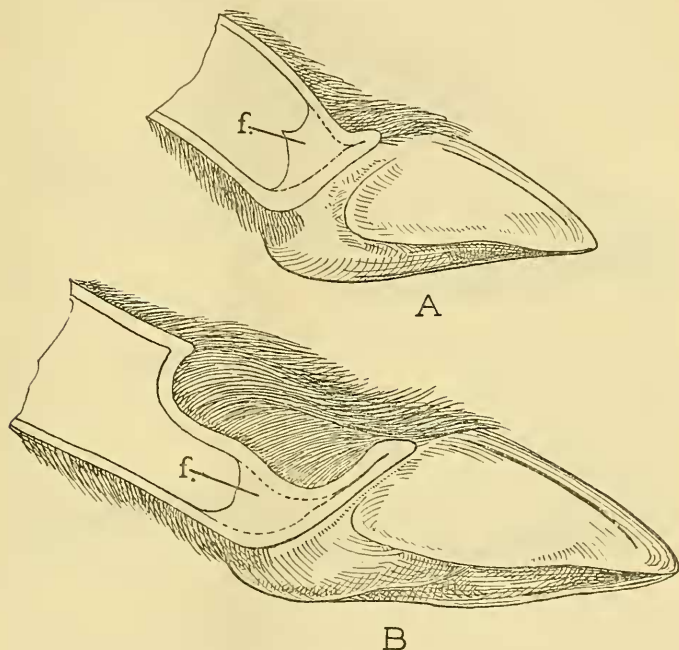
The pedal glands, present only on the front feet, resembled those of *Bubalis caama* in a general way, with the exception that the interdigital pit was much less deep, owing to there being a considerable space between the integument of the back of the pastern and that forming the posterior wall of the cleft; moreover, the skin of the front of the pastern, forming the upper edge of the orifice, was not folded backwards and upwards upon itself, but descended almost at right angles to form the short upper wall of the interdigital cleft. A further difference was seen in the presence of a vertical fascia joining the skin of the back of the pastern to that of the interdigital cleft just above the heels. The walls of the cleft were clothed with long rusty-red hairs, the ends of which projected from the orifice, overhanging the proximal end of the hoof in front.

The hind foot was like that of *B. caama*, except that the depression on the front of the pastern just above the hoof was shallower. A connecting fascia, corresponding to that of the hind foot, was also present.

The area of the preorbital gland on a face-skin of *D. korrigum tiang*, for which I am indebted to Rowland Ward, Ltd., resembled that of *D. k. jimela* in all respects.

The area in question is also bare in *D. hunteri*, *albifrons*, and *pygargus*. In an adult male of *D. albifrons* now living in the Gardens, the gland is usually active and tumid, secreting a substance which passes on to the face, staining the edges of the white blaze yellow. The orifice of the gland is circular and lies in the centre of the smooth glandular swelling. The gland itself, which I saw in a dead Blesbok many years ago, was, I clearly recollect, about as large as a filbert nut, with a short duct leading

Text-fig. 107.

*Damaliscus korrigum jimela.*

A. Median vertical section of hind foot.

B. The same of front foot.

f., fascia.

into it, exactly as in *B. caama*. In two young Bonteboks now living in the Gardens, the gland is much less prominent than in the Blesbok, possibly because the specimens are not yet adult.

The above-described specimen of *D. korrigum jimela* had no inguinal glands; but the hair on the skin a short distance away from the one teat on each side was arranged in a whorl.

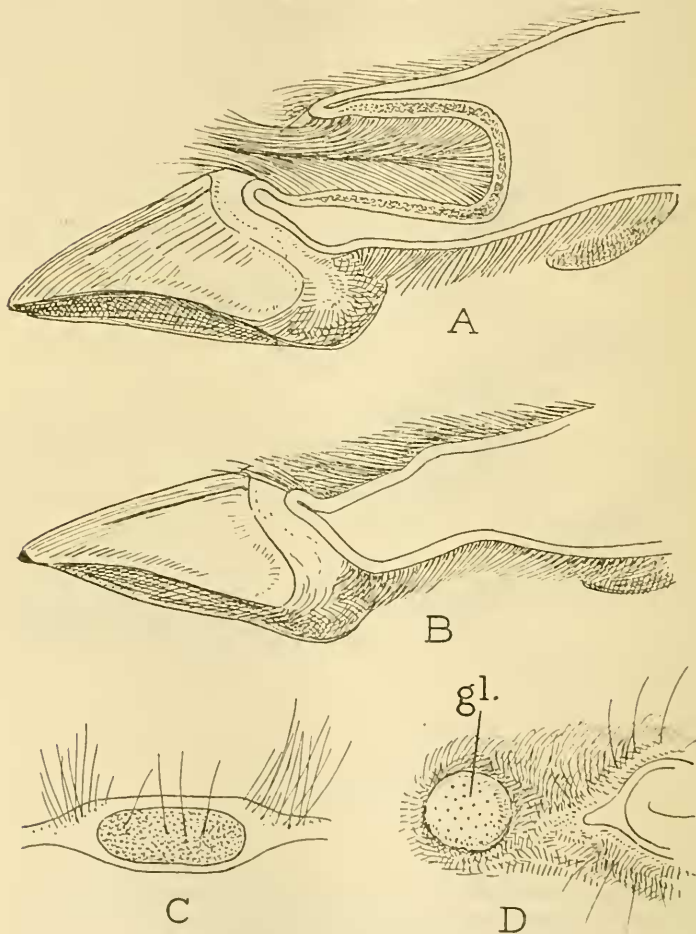
Genus CONNOCHILETES Licht.

CONNOCHILETES GNU Zimm. (The White-tailed Gnu.)

(Text-fig. 108.)

Of this species I have examined two specimens, an immature male and an adult female. In both there were no inguinal glands and a single pair of teats.

Text-fig. 108.

*Connochates gnu.*

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Section of preorbital gland.
- D. Superficial view of preorbital gland (*gl.*).

The preorbital gland consisted of a subcircular patch of black skin, sparsely pitted with setal pores, whence hairs arose. In the young male the gland was as large as a hazel-nut, but markedly longer than deep. In section it was pink in colour and resembled a cyst enveloped in the thickened skin. It was not lodged in any depression of the skull, but merely rested on the bone of the face. The hairs which appeared upon its surface were seen to be rooted deep in the gland and to reach the surface through the pores above described. No secretion could be squeezed from the gland. This was perhaps due to the fact that the animal was immature and had been ailing for some time before death. It seems probable that the secretion naturally exudes through the setal pores. Nevertheless, I have never seen the preorbital gland of a living Gnu, either of this species or of *G. taurinus*, show any sign of secretion or even of moisture. I did not cut the gland of the adult female, since the specimen was required for preservation.

Pedal glands, as in *Bubalis*, are well developed only on the front feet and appear to be absent on the hind feet. The feet and the glands have essentially the same structure as in *Bubalis caama*. In the adult female, however, the cavity of the gland differed in some interesting particulars from that of *B. caama* above described. The posterior wall of the cavity was not folded so closely upon the skin of the interungual web and of the back of the pastern, but ran obliquely upwards and backwards, then turned forwards at a right angle, then downwards and forwards at a right angle closely in contact with the skin of the front of the pastern, which it joined at the upper end of the orifice at a very acute angle, forming a close fold. The anterior upper web thus constituted extended nearly as far downwards as the edge of the interungual web, leaving a much shorter orifice for the gland than in *Bubalis caama*. In the latter the gland was rhomboidal in section, whereas in *C. gnu* it was suboblong. It was thickly clothed with long hairs, projecting like a fringe or tuft from the orifice. The roots of all the hairs were covered and stuck together with blackish secretion smelling exactly like sour milk or cream-cheese. In the young male the cavity of the gland was nearly intermediate in shape between that of the adult and that of *B. caama*, the slit-like orifice being much longer than in the adult owing to the absence of the anterior wall, the anterior web or fold stopping short much higher up the pastern above the hoofs. In section the upper portion of the cavity resembled that of *B. caama*, while its lower portion was like that of the adult *C. gnu*.

On the hind feet there was only a very shallow hair-lined depression, recalling that of *Bubalis caama*.

The front and hind feet of another adult example, kindly given to me by Rowland Ward, exactly resembled the one above described.

Genus GORGON Gray.

GORGON TAURINUS Burch.

(The Brindled Gnu or Blue Wildebeest.)

Living examples of this species have the preorbital gland like that of *Connochates gnu*; and in a dried skin, lent to me by Mr. E. Gerrard, I found the front and hind feet constructed exactly as in that species. One pair of teats only is visible in a pregnant female now living in the Gardens.

Gray long ago placed the White-tailed and the Brindled Gnus in distinct genera; and it was evidently the opinion of Messrs. Sclater and Thomas that there was a great deal to be said in favour of this view, although they did not give it practical expression in their 'Book of Antelopes.' Judged by modern standards it appears to me that the well-known differences between the two are quite worthy of generic recognition. There can be no evasion of this conclusion if specific value be given, as is commonly done, to the differences between the Brindled and White-bearded Gnus. The White-tailed Gnu is a very differently built animal from the two just mentioned. The back is not sloped as in the rest of the Bubalinae, but horizontal, and the hind-quarters are markedly elevated on account of the prominence of the summits of the iliac bones. Other external features separating this species from the Brindled Gnu and from its ally, the White-bearded Gnu (*G. albo-jubatus*), are well known, and are in my opinion equivalent to those separating *Bubalis* and *Damaliscus*.

Using the preorbital glands as a basis, the genera of Bubalinae may be distinguished as follows:—

- a. Preorbital gland marked with a central orifice leading into a hair-lined tube, which dips into the substance of the gland.
 - b. Surface of the preorbital gland naked or nearly so.
- Damaliscus* and *Bubalis lichtensteini*.
- b'. Surface of the preorbital gland thickly and uniformly covered with long hair *Bubalis*.
 - a'. Preorbital gland without any central orifice and tube, its free surface consisting of an area of skin sparsely covered with hairs *Connochates* and *Goryon*.

Since Lichtenstein's Hartbeest, hitherto referred to the genus *Bubalis*, is known to depart from the other species of that genus in the structure of its horns and also in the nakedness of the preorbital gland, it should perhaps be referred to a distinct genus. In diagnosing the genera in this table, no use has been made of the differences recorded in the structure of the pedal glands of *Connochates gnu*, *Bubalis caama*, and *Damaliscus korrigum*, striking though they be, because they have only been noted in a single species of each of the genera.

The structure of the feet and the presence of pedal glands only on those of the anterior pair bear out the evidence from other sources that the Gnus and Hartbeests form a natur a

group. Moreover, it seems to me that the size and structure of the preorbital gland and of the glands in the front feet, coupled with the hairiness of the rhinarium and the presence of a single pair of mammae, suggest tolerably close kinship between *Damaliscus*, the least-specialised member of the Bubalinae, and the Antilopinae. At all events, I think it may be claimed with some assurance that the relationship indicated is closer than that between *Epyceros* and the Antilopinae.

Subfamily ORYGINÆ.

I prefer to use the term Oryginae for the group called Hippotraginae by most modern authors, because the generic name *Hippotragus* will soon, probably, no longer be admitted as a valid generic designation, being antedated both by *Ozanna* and *Elgoceros*.

Genus ORYX Blainv.

According to Owen the following species of this genus have neither preorbital nor inguinal glands: *O. gazella* (= *A. oryx*) and *O. algazel* (= *A. leucoryx*).

Ogilby also says that these two species have neither preorbital nor inguinal glands, but states that the pedal glands are large and that there are two pairs of mammae.

ORYX BEISA Rüpp. (The Beisa.) (Text-fig. 109, C.)

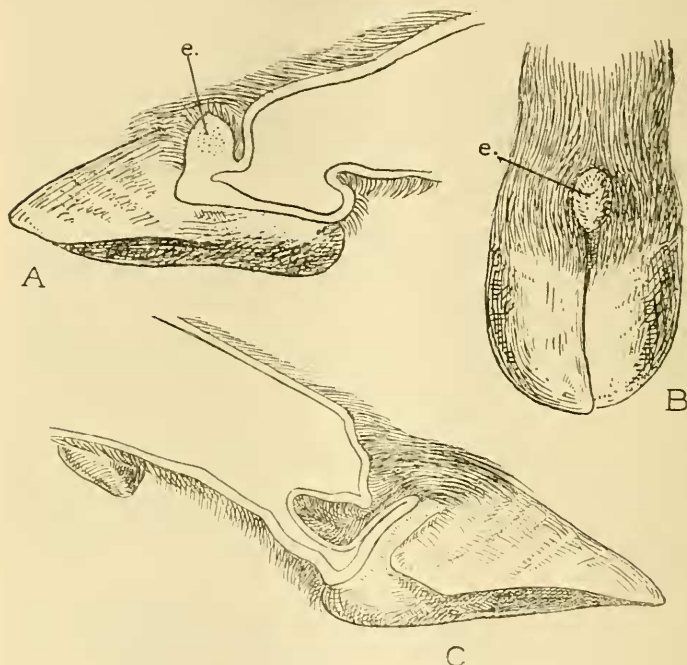
In the dried skin of a young male example of this species, for which I am indebted to Mr. Gerrard, I could find no trace of preorbital glands nor of inguinal glands, but two pairs of mammae were present.

Pedal glands, approximately similar in structure, were present on all four feet. They opened by an elongated, somewhat lanceolate interdigital cleft on the front of the pastern just above the hoofs. This cleft led into a shallow depression, which at its deepest part, close to the interungual web, passed into the principal part of the gland, which consisted of a moderate-sized sac extending for a short distance upwards and backwards almost as far as the posterior integument of the pastern. Describing the gland another way, it might be said to consist of a deep but rather short interdigital depression subdivided into an anterior and posterior part by a ridge of integument projecting from its upper wall, thus constricting its lumen.

The floor and posterior wall of this depression were formed by the closely infolded layer of the interungual web. Its opposite walls were formed by the integument of the front of the pastern, which sloped obliquely downwards and forwards to the aforesaid ridge, then obliquely upwards and backwards. The entire interdigital depression on both sides of the constriction was clothed with longish white hairs clogged with secretion. Inferiorly, just below the orifice, the hairs were longer and overlapped the

proximal edge of the nail of the hoof. The interungual web was thick and horny and, as in the Antilopinae and Bubalinae, extended from the heels to a point near the anterior margin of the hoof before being closely folded upon itself; and, as in the Bubalinae, *Antilope*, *Hippotragus*, and the Tragelaphinae, it was quite smooth.

Text-fig. 109.



- A. Median vertical section of front foot of *Addax nasomaculatus*: *e.*, conical excrescence with the depression behind it.
 B. Anterior view of the same foot; *e.*, conical excrescence.
 C. Median vertical section of hind foot of *Oryx beisa*.

The hoofs were pointed, compressed above, with broad flat heels and flat soles. The only difference noted between the glands of the front and hind feet was the greater development of the constricting ridge in those of the hind feet.

The interdigital glands of *Oryx beisa* with their longer cleft-like orifice occupy a nearly intermediate position between those of Gazelles and those of *Hippotragus*.

ORYX LEUCORYX Pall.

(The White Oryx = *O. beatrix* of most authors.)

In an old dried skin of a male example from the shores of the

Persian Gulf, kindly lent to me by Mr. Gerrard, the pedal glands, though imperfect, had apparently the same structure as in *O. beisa* and there was no trace of inguinal glands.

ORYX ALGAZEL Oken.

(The Soudanese Oryx = *O. leucoryx* of most authors.)

Both Owen and Ogilby state that this species has no pre-orbital gland. I presume this observation was based upon an examination of dried skins or of skulls. It is not, however, true; for in the example now living in the Gardens there is quite commonly a small patch of secretion sticking the hairs together about an inch in front of the eye. This proves the existence of a specialised glandular area beneath the hairs; but probably the gland is not highly developed.

Genus HIPPOTRAGUS Sund.

According to Owen, the following species of this genus have neither preorbital nor inguinal glands: *H. leucophaea*, *equina* (= *barbata*).

The only species of this genus examined by Ogilby was *H. leucophaea*, which he referred to the genus *Oryx*. He agreed with Owen that this species has neither inguinal nor preorbital glands, but adds that the pedal glands are large and that there are two pairs of mammae. W. L. Schlater also states that in the genus *Hippotragus* the preorbital gland is absent and that there are two pairs of mammae.

HIPPOTRAGUS NIGER Harris. (The Sable Antelope.)

(Text-fig. 110.)

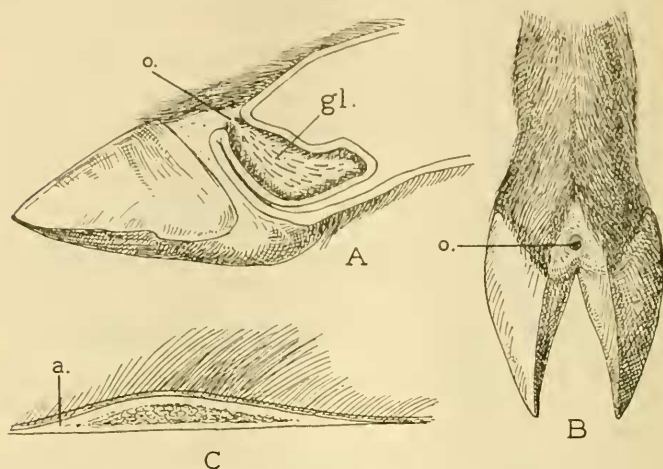
In an adult female of this species which died in the Gardens I found a preorbital gland underlying the white preorbital tuft of hair. It was very little differentiated, however, consisting, like the knee glands of Gazelles and some Sheep, of thickened vascular integument. The bases of the white hairs were crowded with pale yellow grains like scurf, smelling of a mixture of sour milk and new-mown hay.

There were no inguinal glands.

The pedal glands were well developed on all four feet and opened to the exterior by a small subcircular orifice in the centre of a naked patch of skin in a shallow depression close to the proximal end of the hoofs. The gland was a large sac passing obliquely upwards and backwards and reaching as far as the posterior integument of the pastern, and with its lower wall closely applied inferiorly to the interungual web which was sharply folded back upon itself, the infolded portion constituting the wall of the gland in question. The walls of the gland were covered with short hairs, becoming longer towards the orifice of the gland.

The interungual web of the hoof was smooth from the orifice of the gland to the posterior area of the heels.

Text-fig. 110.



Hippotragus niger.

- A. Median vertical section of front foot: *gl.*, pedal gland; *o.*, its orifice.
 B. Anterior view of front foot: *o.*, orifice of gland.
 C. Longitudinal section of preorbital gland; *a.*, ocular end of gland.

I was able to verify these facts upon a second specimen, a dry skin kindly lent to me by Mr. Gerrard. This specimen had two pairs of teats, but no trace of inguinal glands was discoverable.

HIPPOTRAGUS EQUINUS Is. Geoff.

(The Roan Antelope.)

In a female specimen with two pairs of teats, but no inguinal glands, for the examination of which I am indebted to Mr. Gerrard, I found the pedal glands to be of substantially the same structure as in *H. niger*, except that there was a slight constriction of the lumen of the gland, caused by a small integumental ridge rising from its upper wall and partly dividing it into an outer and an inner chamber, as in *Oryx beisa*.

Genus ADDAX Raf.

ADDAX NASO-MACULATUS Licht. (The Addax.)

(Text-fig. 109, A, B, p. 908.)

According to Owen, this species has neither preorbital nor inguinal glands.

I have seen only the front and hind feet of one dead example, no other material being available.

The feet were very different from those of *Oryx* and *Hippotragus*, being low, flat, long-heeled, and broad at the point in adaptation to a soil of soft sand. In section, the integument of the posterior surface of the pastern was seen to be folded just above the heels like that of *Pantholops*. From that point it passed forwards for some distance parallel with the sole of the foot before turning abruptly upwards towards the front of the pastern. Here it passed into a somewhat conical excrescence or eminence, covered with short hair and defined behind and laterally by a semicircular infolding or depression of the skin. Behind this excrescence, the integument of the anterior surface of the pastern was continued straight up this area without sign of insinking and was covered with normal longish hairs. The latter inferiorly encircled the excrescence, which jutted up like an island from their midst. I believe the excrescence to be glandular. The structure of the two feet was the same, except that the excrescence was smaller on the foot which I judged to belong to the hind leg.

Examination of the feet of a very young example now living in the Gardens revealed no signs of the excrescence, but there was a distinct orifice, representing, I suppose, the infolding of the skin defining the excrescence in the adult. This orifice was in almost the same position as the orifice of the gland in *Oryx*, and its glandular nature was attested by the staining yellow of the white hairs round it.

Addax has a marked patch of longer hairs below the eye on each side of the face. This probably overlies a glandular thickening of the skin, such as is present in *Hippotragus*. I have, however, no direct evidence of the fact.

From the structure of the feet *Addax* would seem to be less closely allied to *Oryx* and *Hippotragus* than these two are to one another. But more and better material of the genus must be examined before any satisfactory conclusion as to its true systematic position can be arrived at.

Subfamily CERVICAPRINÆ.

Genus PELEA Gray.

PELEA CAPREOLUS Bechst. (The Vaal Rhebok.)

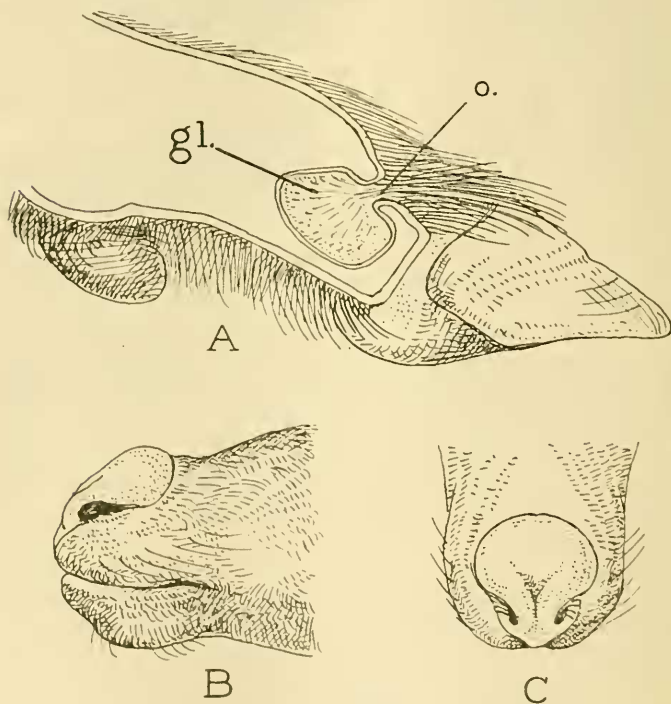
(Text-fig. 111.)

According to Owen, this species possesses inguinal glands, but has no preorbital glands.

The absence of preorbital glands has been affirmed by subsequent authors, and correctly so, judging from the one specimen of this species I have examined, a female brought by Dr. Lyster Jameson from S. Africa, which lived two years in the Gardens. This specimen, however, had no trace of inguinal glands. Pedal glands were well developed on all four feet. They opened by a

small circular orifice on the front of the foot in a shallow depression lined with long hairs. The orifice led into a short hair-lined duct which expanded into a capacious but laterally compressed thin-walled sac reaching almost to the posterior integument of the fetlock. The sac was filled with semifluid, pale-coloured, evil-smelling secretion, recalling exactly the odour of dog's dung. Close to the orifice in the depression arose a number of long hairs overhanging the base of the hoofs in front, and these were stuck together with the secretion, which could be easily squeezed from the gland by pressure applied to the sides of the pastern.

Text-fig. 111.

*Pelca capreolus* ♀.

A, Median vertical section of hind foot: *gl.*, pedal gland; *o.*, its orifice.
B & C, Lateral and dorsal views of the nose to show swollen rhinarium.

The structure of the feet was almost the same as in *Cervicapra redunca*, the interungual integument being quite naked, meeting that of the back of the pastern at a right angle and forming an obtuse angle with the floor of the depression on the front of the fetlock. Thus the integument or "web" joining the hoofs

together extended from the heels almost up to the proximal end of the anterior ridge of the nail. The apical angle of the nail was also less acute than in *Cervicapra redunca* and *Adenota kob*, the hoofs more approaching those of Goats and Sheep in shape—in accordance, no doubt, with the mountain habitat of *Pelea*.

A well-known distinguishing feature of *Pelea* as compared with *Cervicapra* and *Kobus* is the enlarged and swollen rhinarium, which has a widely rounded posterior border extending backwards beyond the posterior notch of the nostril. This rhinarium is glandular. In the living animal it became studded with drops of moisture under the stimulus of excitement or pleasure, and after death was easily made by pressure to yield the same substance.

Like *Cervicapra* and *Kobus*, *Pelea* has two pairs of mammae.

Genus CERVICAPRA Blainv.

Owen noticed the absence of preorbital and the presence of inguinal glands in three species of this genus, namely, in *C. redunca*, the Nagor, a Senegambian species; in *C. arundinum*, which he quoted as *Antilope eleotragus*; and in *C. fulvorufula*, if I am right in supposing he meant this species by *A. landiana*, the latter name being, I surmise, written in error for *lalandia* or *lalandii*.

I have examined only fresh material of one species, namely the following.

CERVICAPRA REDUNCA Pall. (The Nagor.)

(Text-fig. 112.)

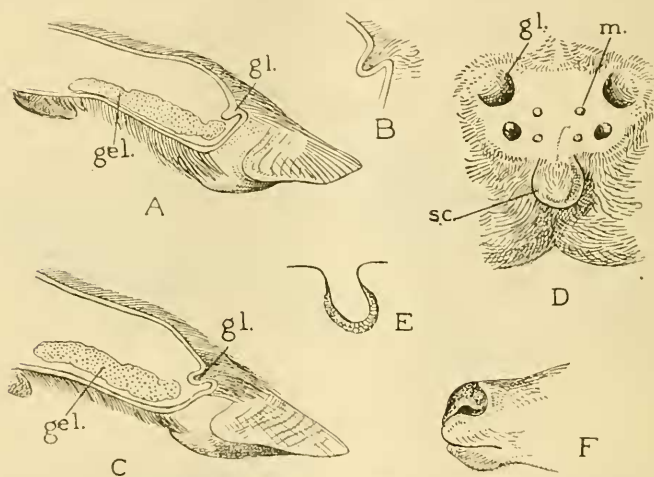
Owen does not state how many inguinal glands he discovered in the species he examined, but in two examples of *C. redunca*, from Senegambia, presented by Sir George Denton, I found two pairs of sacs. The anterior sac on each side was wide-mouthed but shallow, the glandular area into which it dipped being only slightly vascular. The posterior sac, lying rather nearer the middle line and close to the scrotum, was, on the contrary, $1\frac{1}{2}$ inches deep, of even width throughout, the orifice being about $\frac{1}{2}$ an inch in diameter and not half the width of the orifice of the anterior sac. Its glandular area was very thick and vascular. Both pouches secreted a semifluid substance, turning yellow and waxy at the orifice and giving off an odour of flour-paste going stale, which to me was most nauseous.

There were no preorbital glands.

In one specimen I found no trace of pedal glands; but in the other there was a very small hair-lined pouch opening into the shallow hair-lined depression on the front of the pastern just above the angle formed by the junction of the integument of this surface with the strip of naked skin extending from the front to the heel of the hoofs and binding the two together. There

appeared to be no gland connected with this pocket, since there was no secretion on the hairs projecting from its orifice; but beneath the pocket between the phalanges there was an elongated mass of vascular gelatinous tissue extending almost as far up as the false hoofs, just such as is found in the hoofs of Oxen. The fore and hind feet were alike, except that the anterior depression was somewhat deeper on the hind feet, allowing a slightly wider spread to the hoofs, and whereas the false hoofs were united by thick horny material on the fore feet, those of the hind feet were connected by naked skin.

Text-fig. 112.

*Cervicapra redunca.*

- A. Median vertical section of front foot taken a little to one side of the aborted gland (*gl.*); *gel.*, gelatinous interdigital mass.
- B. The aborted gland of the same in section.
- C. Median vertical section of hind foot: lettering as in A.
- D. Inguinal region showing four mammae (*m.*); scrotum (*sc.*) and inguinal glands, the anterior pair (*gl.*) wide and shallow, the posterior pair behind them narrow and deep.
- E. Section of inguinal gland of posterior pair.
- F. Side view of nose to show rhinarium.

In both specimens there were two pairs of mammae; but in neither was there a bare patch of skin below the ear. The knees had a bare patch of thickened horny skin, which was apparently, however, not glandular. So far as the pedal glands are concerned, the genus *Cervicapra*, as represented by *redunca*, stands in the same relation to *Pelea capreolus* as *Capra* stands to *Oris*; and there cannot, I think, be much doubt that the ancestors of existing species of *Cervicapra* are descended from Antelopes with pedal glands like those of *Pelea*.

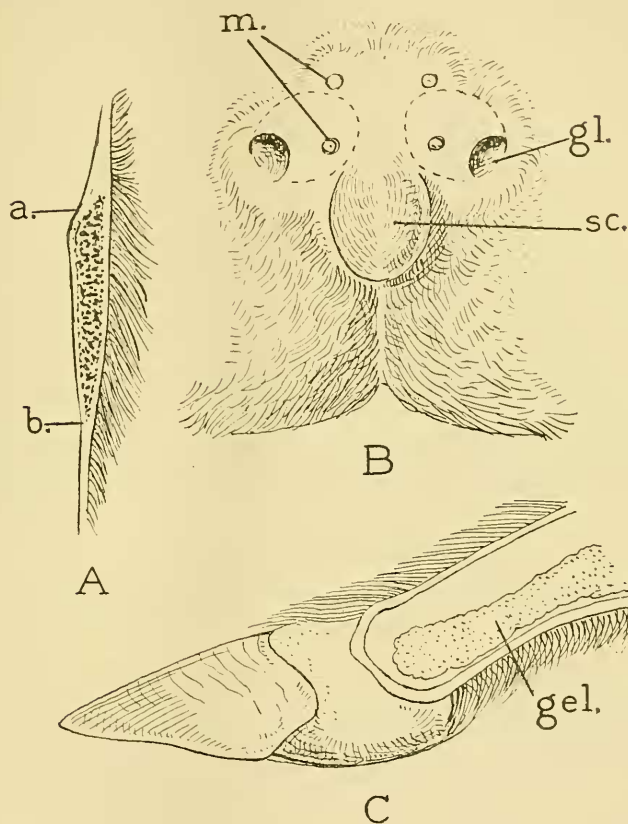
Genus ADENOTA Gray.

ADENOTA KOB Ertl. (Buffon's Kob.)

(Text-fig. 113.)

According to Owen, this species has inguinal pits but no preorbital glands.

Text-fig. 113.

*Adenota kob.*

- A. Longitudinal section of preorbital gland: *a*, upper or ocular end; *b*, lower end.
 B. Inguinal region: *m.*, mamme; *sc.*, scrotum; *gl.*, orifice of gland, the subcutaneous extension of which is shown by the dotted line.
 C. Median vertical section of front foot; *gel.*, gelatinous interdigital mass.

I have seen two examples of this species, a subadult male from Upper Nigeria presented by Lady Constance Stewart Richardson,

and an immature female from Sierra Leone presented by Mr. Tinling.

In the female there was a distinct preorbital gland, marked externally by a tuft of hair darker in colour and a little longer than that of the surrounding area. Beneath this the skin was considerably thickened, the thickest part being situated above towards the anterior angle of the eye and the thinnest part below, where the thickening gradually merged with the normal skin of the cheek. In its essential characters this gland resembled that of the Sable Antelope above described (p. 910). The male was not examined for this character.

Both specimens had two pairs of teats and a single pair of inguinal glands representing the posterior pair found in *Cerri-capra redunca*; but in addition to these there was upon the right side in the female a very minute pocket lying far out and in advance of the mammae. There was no trace of this on the left side. The orifice of the large gland was subcircular, about $\frac{1}{2}$ an inch in diameter in the male and $\frac{1}{4}$ of an inch in the female; the pouch itself was capacious, widening considerably within the orifice and extending for 1 inch in the female and $1\frac{1}{2}$ inches in the male in the direction of the scrotum and mammae. The yellow secretion had exactly the same nauseating smell as that of *Cerri-capra redunca*, namely of flour-paste or starch. There were no pedal glands and no trace even of the duct. The structure of the feet was the same as in *Cerri-capra redunca*, with the same elongated mass of vascular gelatinous tissue lying between the penultimate phalanges along the inner surface of the skin of the back of the pastern. The skin round the false hoofs was naked.

Genus KOB'S Smith.

KOBUS ELLIPSIPRYMNUS Ogilby, DEFASSA Rüpp., and MARLE Gray.
(Water Bucks.)

According to Owen, *K. ellipsiprymnus* has neither preorbital nor inguinal glands.

It is on account of the alleged absence of the inguinal glands in this species and their presence in *A. kob* that I keep the two species under separate generic headings. Trouessart regards them as representing distinct subgenera, presumably for other reasons.

On the skin of the head of an example of *K. defassa*, from the White Nile, lent to me by Rowland Ward, Ltd., I could find no trace of a preorbital gland; but I think a gland resembling that of *Adenota kob* will probably be found when fresh material is examined. The fore and hind feet of *K. marie* (Mrs. Gray's Water Buck), given to me by Mr. Gerrard, showed no trace of pedal glands, the feet in section resembling those of *A. kob*.

The genera of this subfamily, so far as my observations extend,

may be distinguished as follows, using the glands as a basis for their separation :—

- a. Pedal glands present on all four feet and opening by a short duct with a small circular orifice on the front of the pastern just above the hoofs; summit of rhinarium swollen and glandular, and extending back beyond the posterior edge of the nostrils; no inguinal glands *Pelea*.
- a'. Pedal glands represented at most by the duct of the glands present in *Pelea*; summit of rhinarium normal, not extending behind the posterior notch of the nostrils.
 - b. With two pairs of inguinal glands; tail bushy as in *Pelea*... *Cervicapra*.
 - b'. Inguinal glands absent or represented by a single pair of pouches; tail tufted at the end.
 - c. A single pair of inguinal glands *Adenota*.
 - c'. No inguinal glands *Kobus*.

In their volume on the Mammalia, Flower and Lydekker classified the genera above referred to the Cervicaprinæ with the Neotraginæ. The Cervicaprinæ, however, differ markedly from the Neotraginæ, so far as my observations extend, in the structure of the feet, since they entirely lack the deep and long interdigital cleft on the front of the pastern found in the Neotraginæ.

It seems to me that, in looking for the relationships of the Cervicaprinæ on the lines followed in this paper, the following facts should not be ignored. With the exception of the Indian genera of Tragelaphinæ, the preorbital gland is absent in that group; and in the Cervicaprinæ it is at most represented by an integumental thickening. In both groups, and in no other subfamilies of Bovidæ, two pairs of inguinal pouches have been recorded. More significant still is the fact that the structure of the feet, whether pedal glands be present or absent, is the same in the Cervicaprinæ as in the Tragelaphinæ. Corroborating these characters are the presence of two pairs of mammae and a moderate or large rhinarium, to which may be added the invariable absence of horns in the females of Cervicaprinæ and in most genera of Tragelaphinæ. I do not, however, attach much importance to this character, despite the value given to it by some writers*.

At all events, it must, I think, be conceded that the Cervicaprinæ are more akin to the Tragelaphinæ than they are to the Antilopinæ, Bubalinæ, Neotraginæ, Cephalophinæ, or Oryginæ, although the retention by *Pelea* of pedal glands, somewhat recalling those of the Oryginæ, is a fact full of interest.

The following genus is possibly related to the Cervicaprinæ (see p. 897).

Genus AMMODORCAS THOS.

AMMODORCAS CLARKEI THOS.

(The Dibatag or Clarke's Gazelle.)

The only materials of this genus and species I have seen are

* W. L. Slater, for instance, who uses it as a basis for grouping the S. African subfamilies of Bovidæ.

some dried skins in the British Museum. I made, however, no dissections. Superficially the feet showed no trace of pedal glands. Certainly there were none such as exist in the Antilopinae; and I judged that the feet resembled those of *Æpyceros* or *Kobus*. Also there were two pairs of well-developed teats, and I could find no evidence of the existence of inguinal glands. These features, coupled with the long "bovine" tail and the shape and direction of the horns, which are more Cervicaprine than Gazelline, should exclude the genus from the Antilopinae. On the other hand, the preorbital glands appear to be like those of *Gazella*, and the muffle is hairy as in that genus. The skull also is very Gazelline.

These cross-resemblances make *Ammodorcas* extremely difficult to classify. It has been described as intermediate between *Gazella* and *Lithocranius*. This is true of the length of the neck, the structure of the upper lip, and some characters connected with the skull. On the other hand, in the structure of the feet, horns, and tail, the genus is less Gazelline than *Lithocranius*; and I am disposed to think that the degree of relationship to *Gazella* that the two exhibit may be fairly gauged by the fact that the type-species of *Lithocranius* was referred to *Gazella* by so high an authority as Sir Victor Brooke, and was for a long time cited under that genus; while the type-species of *Ammodorcas* was originally assigned on equally good authority to the genus *Cervicapra*. From this it may be inferred that the kinship between *Lithocranius* and *Gazella* is tolerably obvious and that between *Ammodorcas* and *Gazella* by no means evident.

Subfamily ÆPYCERINÆ.

Genus ÆPYCEROS Sund.

ÆPYCEROS MELAMPUS Licht. (The Impala or Pallah.)

(Text-figs. 114, 115.)

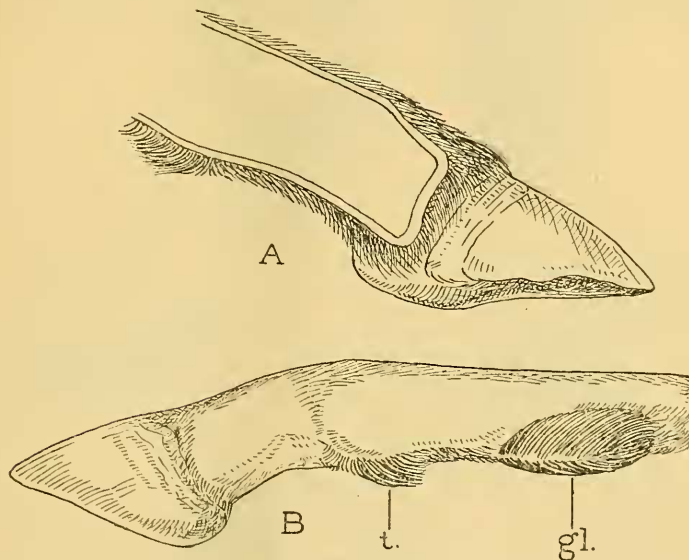
According to Owen, this species has large preorbital glands and inguinal glands as well. All recent authors, however, are in agreement that there are no preorbital glands, and I could find no trace of them on any of the dried skins in the collection of the British Museum.

I am indebted to Messrs. Rowland Ward, Ltd., and to Mr. E. Gerrard for the opportunity of examining and cutting open the hind feet of two specimens, and of thus being able to establish the absence of pedal glands on these limbs; and, so far as I can judge from looking at the fore feet of skins in the British Museum, they are equally absent in the front legs, the feet of which seem to be constructed exactly like those of the posterior pair except for the absence of the two metatarsal glands, well known and often recorded as present on each hind leg.

Of these glands W. L. Slater says: "attached to the lower ends of the cannon-bones of the hind legs is a brush of very dark brown

hairs surrounding the opening of a peculiar gland containing a fatty secretion." This is not quite an accurate description of the glands, according to my observations. The long blackish hairs marking each gland form a subelliptical elongated mat. The hairs point downwards, but those on each side of the middle line of the mat are inclined inwards, meeting at their tips and marking a central streak. When these converging hairs are pulled on one side it may be seen that they overlap an elongated area of naked skin, broadest across the middle, pointed above and below, and more than twice as long as wide. This naked area was covered, in the specimen examined, with secretion and the skin composing

Text-fig. 114.

*Æpyeros melampus.*

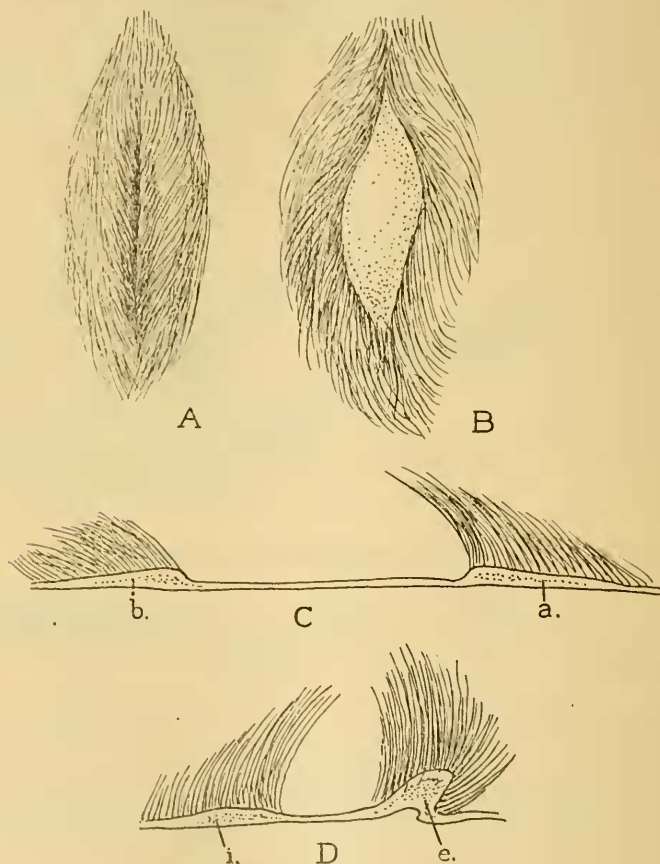
- A. Median vertical section of hind foot.
 B. Hind foot to show the mat of hairs (*gl.*) marking one of the metatarsal glands and the tuft (*t*) representing the false hoofs.

it was shown in section to be exceedingly thin. The skin surrounding it was, however, markedly thickened, especially externally, where it formed a distinct upstanding ridge. It was upon this thickened skin that the long hairs forming the mat grew; and, since the bases of these hairs were clogged with secretion, I infer that the thickened rim of skin is the secreting area of the gland and that the depressed naked area constitutes the floor of a kind of reservoir for the secretion, which is conducted downwards by the downward-growing long hairs.

The area of the false hoofs, which are themselves absent, is

covered with a thick mat of longish mostly black hairs directed backwards and upwards. The skin beneath this mat was thick and horny, but I could not find any evidence either upon the hairs or in the skin of special glandular development.

Text-fig. 115.

*Npyceros melampus.*

- A. One of the metatarsal glands with the hairs undisturbed.
- B. The same with the hairs pulled aside to show the area of naked skin beneath.
- C. Longitudinal section of the gland: *a*, its upper, *b*, its lower end.
- D. Transverse section of the same: *e*, its external, *i*, its internal edge.

The feet themselves were constructed as in the Tragelaphinæ and most Cervicaprinæ, except that the whole interungual integument, forming the web, was covered with short hairs from front to back.

Although Gray long ago made the genus *Epyceros* the type of a special family, it has of late years found a place amongst the Antilopinae. Apart, however, from the hairiness of the rhinarium and of the interungual integument of the feet, it has very few "Antilopine" features, in the strict sense of the word. This latter feature, moreover, is as much Neotragine as Antilopine. In other respects, the feet may be described as Tragelaphine or Cervicaprine, except for the disappearance of the false hoofs and the presence of the metatarsal glandular mats of hair. The horns moreover, are as much Cervicaprine as Antilopine in character, and the absence of the preorbital gland is another feature excluding the genus from the Antilopinae.

Hence, taking into consideration the sum total of its characters, the peculiarities of *Epyceros* seem to me to be best expressed by setting it in a subfamily apart from all others.

Subfamily TRAGELAPHINÆ.

Genus TETRACEROS Leach.

TETRACEROS QUADRICORNIS Blainv.

(The Four-horned Antelope.)

(Text-figs. 116, A, B; 117, 118, 119, A, B, C.)

Hodgson described the preorbital glands of the genus *Tetraceros* as linear and longitudinal, and stated that inguinal glands are absent and pedal glands absent or present only on the hind feet. Blanford repeated this account with the additional information that the pedal glands are confined to the hind feet.

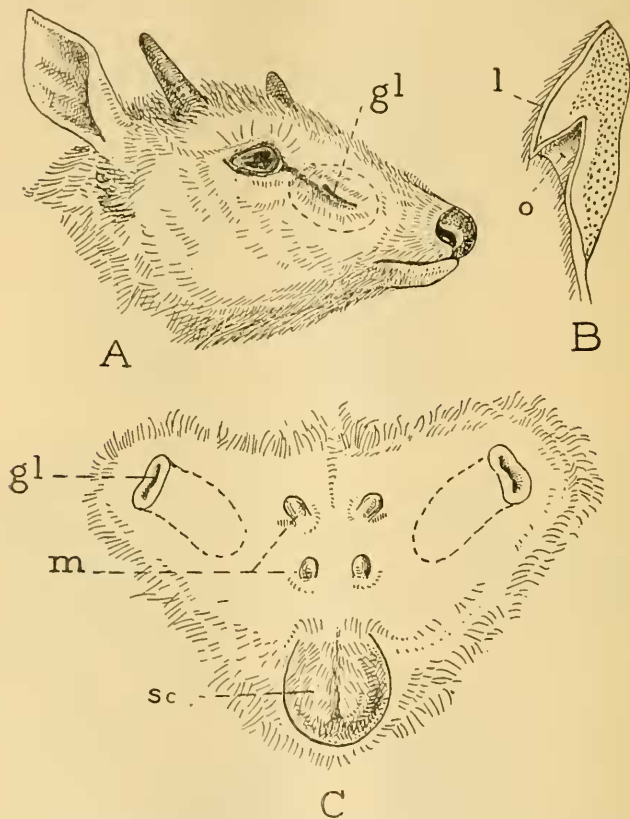
I have seen three examples of this species, a still-born young one and an adult male and female. In all the preorbital gland was well developed and valvular, consisting of a longitudinal pocket, the upper rim of which was produced into a large overlapping flap, forming a longitudinal slit where its free margin came into contact with the skin below it. When the flap was lifted a blackish nearly naked area was exposed; the posterior or ocular end of this area was the deepest portion of the invagination, which from that point forwards became gradually shallower. The gland itself was thick and pale in colour. In the adult male it was much larger than in the adult female, and in the summer discharged a quantity of soft cheesy-yellow secretion. The odour of this was not noted after death, the specimen having been preserved in alcohol; but in the fresh female specimen the drops of clear fluid that were squeezed from the gland had a faint aromatic scent.

There were two pairs of teats, but no trace of inguinal glands.

The feet were constructed as in the genus *Tragelaphus*, the hoofs being short and but little distensible, owing to the extension of the interungual integument from the heels forwards for some distance before curving backwards to join that of the front of the

pastern, merely a shallow depression being formed. There was no trace of any folding of the integument constituting an interdigital cleft or gland such as is seen in the *Cephalophinae*, *Antilopinae*, and *Neotraginae*. The interungual skin, moreover, was

Text-fig. 116.

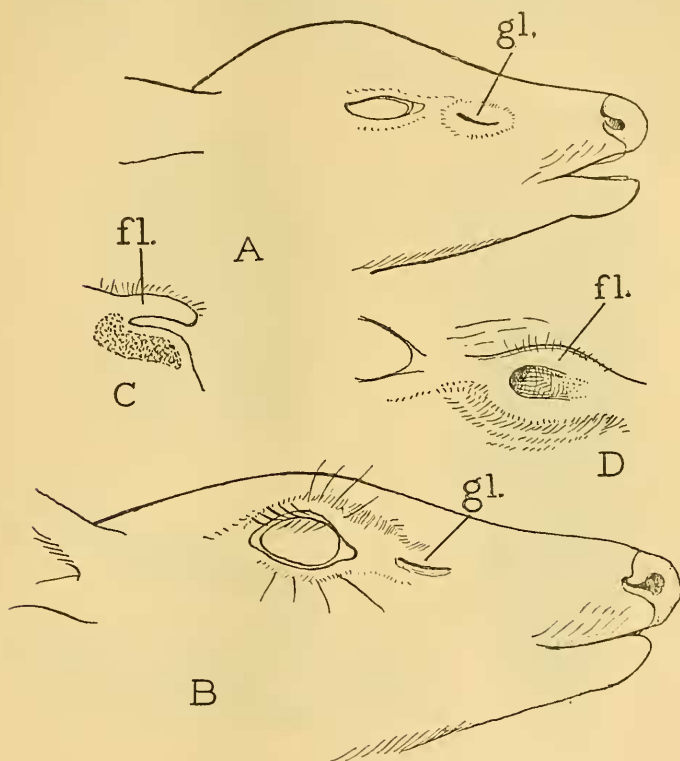


- A. Head of *Tetraceros quadricornis* ♂: orifice of gland (*gl.*); area of gland represented by dotted line.
 B. Transverse section through the gland; *o*, its orifice; *l*, flap of skin constituting its upper lid.
 C. Inguinal region of *Tragelaphus scriptus scriptus* ♂: *m.*, mammae; *sc.*, scrotum; *gl.*, orifice of gland; the subcutaneous extension of the gland shown by a dotted line.

naked. In the male there was a small accumulation of material on the hairs in the shallow depression of the front of the pastern just above the smooth area of the interungual integument; but there was no evidence that this was an odorous secretion. In the adult female, a much older animal, however, there was on all four

feet a large black horny excrescence occupying the same position and large enough to be visible without separation of the hoofs. The skin from which this excrescence arose was thrown into a multitude of columnar folds. Since I have seen no such excrescence on the feet of any other specimen of this Antelope, I must regard its development in this example as abnormal, perhaps pathological.

Text-fig. 117.

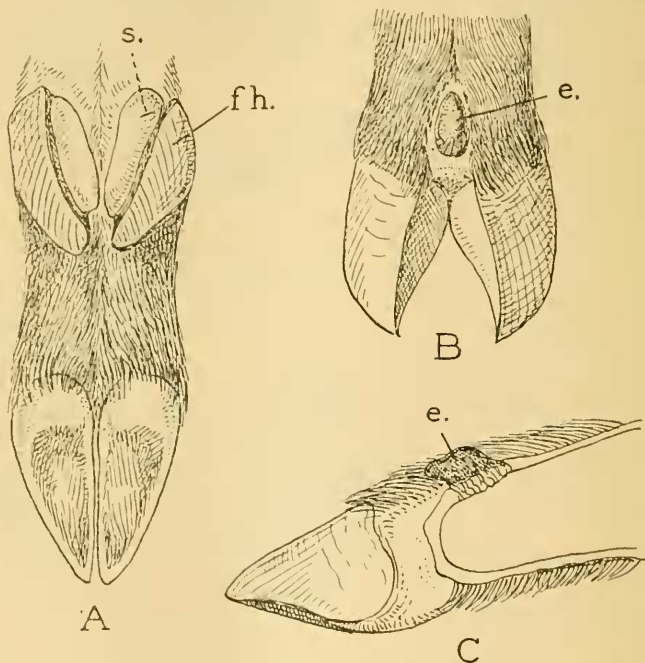
*Tetraceros quadricornis.*

- A. Head of newly born young: *gl.*, preorbital gland.
- B. Head of female: *gl.*, preorbital gland.
- C. Section of the preorbital gland of the same: *fl.*, flap of skin constituting its upper lid.
- D. Preorbital gland of the same with the lid (*fl.*) raised.

One of the most interesting features connected with this genus is the presence of a pair of well-developed glands between the false hoofs of the hind legs. In both the male and the female the false hoofs were large and the skin between them was black, tumid, horny, but soft and naked, except for a longish fringe along

the middle line. When squeezed a yellowish buttery substance with a strong sour odour exuded from a pair of smallish apertures, one on each side close to the middle line, so that the hairs became clogged with it. This aperture led into a voluminous sac, very scantily clothed with short pale hairs, the two sacs being separated by a narrow partition and occupying otherwise the whole area between the two false hoofs. Each was filled with the odorous substance above-mentioned, which, in the male at least, presented a concentrically stratified arrangement and was greenish in colour.

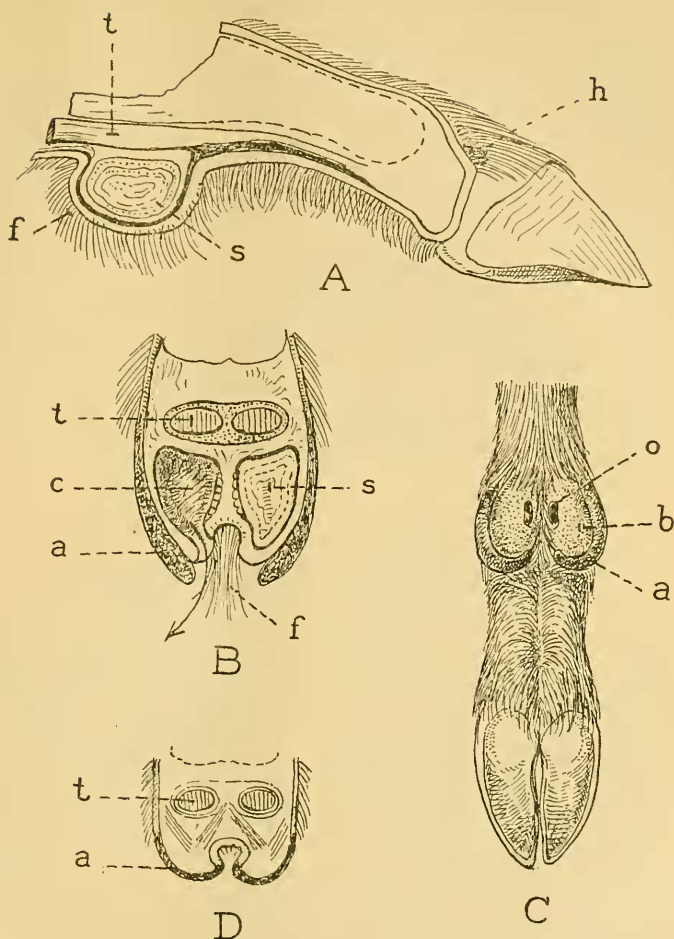
Text-fig. 118.

*Tetraceros quadricornis* ♀.

- A. Inferior view of hind foot: *fh.*, false hoof with its inner half and the adjacent skin cut away to show the glandular mass (*s.*).
- B. Front view of the same foot showing the large horny accretion (*e.*).
- C. The same in median vertical section.

This is the only Antelope known to me which possesses such glands. Whether these sacs are the glands that Hodgson mentioned as sometimes present in the hind feet or not I cannot say. In any case, it is quite evident that they have no sort of connection, except a functional one, with the interdigital glands of other Bovidae.

Text-fig. 119.



- A. Median vertical section of hind foot of *Tetracerus quadricornis* ♂: *t*, tendon; *h*, small horny accretion at anterior end of interungual web; *f*, fringe of hair between false hoofs; *s*, secretion within the sac shown by cutting away the partition between the two glands.
- B. Transverse section of the pastern of *T. quadricornis* ♂, through the false hoofs: *t*, tendon; *c*, glandular sac with arrow marking the orifice; *a*, false hoof; *f*, fringe of hair between the glandular areas of the false hoofs, with the partition above it; *s*, secretion within the other sac, the orifice of which is not seen.
- C. Inferior view of hind foot of *T. quadricornis* ♂: *a*, false hoof; *b*, horny but soft integument forming lower wall of gland; *o*, orifice of gland.
- D. Transverse section through the region of the false hoofs of *Tragelaphus scriptus* ♂, for comparison with B: *t*, tendon; *a*, false hoof.

Tetraceros is usually regarded as belonging to the Cephalophinae. I do not think, however, that the evidence for this relationship is strong. *Tetraceros* and *Cephalophus* differ widely in the structure of the feet and of the preorbital glands; but *Tetraceros* approaches *Boselaphus* in these particulars. The presence of four mammae, the absence of inguinal glands, and the size of the muzzle may also be cited as corroborative evidence of this relationship. Most suggestive, too, is the presence of white patches on the pasterns, and sometimes at all events of two white specks on the cheeks in *Tetraceros*. When I noticed these marks in the living animal, before a dead one was available for examination, I felt sure that the affinities of the genus would prove to be with the Tragelaphines, a group in which these markings are extraordinarily persistent. I subsequently found that Sir Harry Johnston* had noticed the same colour-features in *Tetraceros*, and pointed out the resemblance the genus presents to the Tragelaphines in those particulars. It is true that the horns of *Tetraceros* have no anterior crest or keel; nevertheless, they are more like the horns of *Boselaphus* than the latter are like the spirally twisted horns of the African Tragelaphines.

Genus BOSELAPHUS Blainv.

BOSELAPHUS TRAGOCAMELUS Pall. (The Nyghaie.)

(Text-figs. 120, 121.)

According to Owen, this species has inguinal glands; Ogilby, on the contrary, says they are absent. The two authors agree, however, as to the presence of preorbital glands; and Ogilby adds that there are distinct pedal or interdigital glands. Blanford supports Ogilby's statements.

Turner described † the preorbital gland as a slight pit immediately in front of the orbit with a small longitudinal fold of skin in front of it. In the middle of this fold (or flap) of skin "there is a small round pore, through which exudes a yellowish secretion furnished by a gland placed just underneath. The gland itself is slightly larger than a hazel-nut and is laid upon the surface of the bone without any fossa to receive it."

In an adult female example kindly sent to me by the Duke of Bedford, K.G., I found the preorbital gland marked externally by a short longitudinal slit some distance in front of the eye, the area round the slit and between it and the corner of the eye being practically naked. When opened, this slit was seen to be the orifice of a shallow elliptical depression containing some dried waxy secretion. Near the centre of the depression, but varying in position on the two sides, was a conspicuous circular hair-follicle with a hair protruding from it. There were also one or two

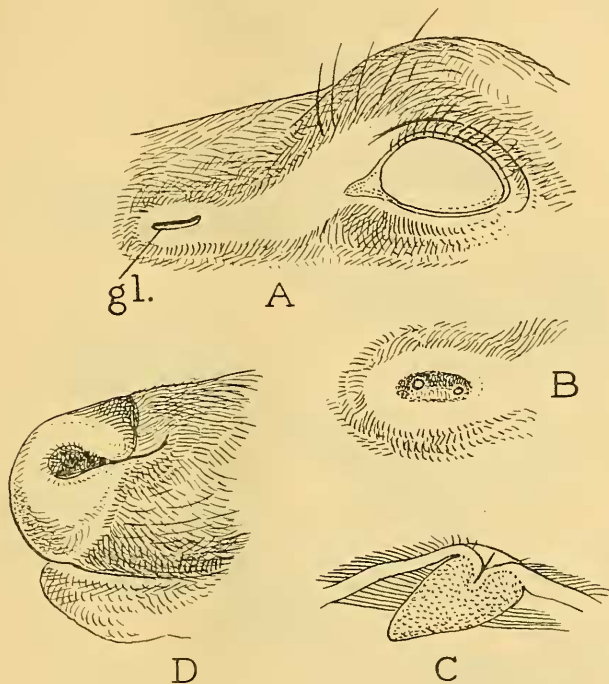
* 'Liberia,' ii. p. 738, 1906.

† P. Z. S. 1851, p. 116.

additional but smaller hair-follicles, also varying in position. From these follicles yellow waxy secretion could be squeezed; but I could detect no special odour about the secretion. As described by Turner, the underlying glandular mass was of large size and elongated, but heart-shaped in transverse section. Its colour was yellowish.

There were two pairs of teats, but no trace of inguinal glands could be detected.

Text-fig. 120.



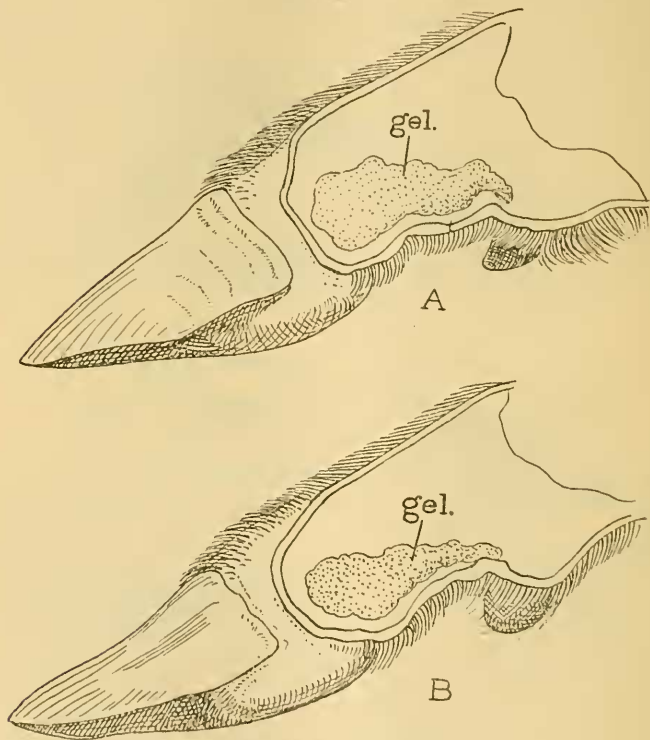
Boselaphus tragocamelus ♀.

- A. Portion of the face showing the eye and the orifice of the preorbital gland (*gl.*).
- B. Preorbital gland with the lid raised showing two large hair follicles.
- C. Section of the gland passing through the larger hair follicle showing the protruding bristle.
- D. Rhinarium.

The feet were constructed exactly as in other Tragelaphinae, the interungual integument being smooth from the heels forwards towards the proximal edge of the nail in front, then inclined obliquely upwards to meet that of the anterior surface of the pastern, leaving a small smooth triangular area at the bottom of the pastern in front just above the hoofs. Between

the phalanges of the pastern was the gelatinous mass of tissue found in *Taurotragus*, *Bos*, and *Kobus*. In connection with the relationship here claimed between *Boselaphus* and *Tetraceros*, it was especially interesting to note that the skin between the false hoofs of the hind feet was white, thick, and highly glandular, the hairs being packed with secretion, smelling like the fat of tallow candles.

Text-fig. 121.

*Boselaphus tragocamelus* ♀.

- A. Median vertical section of hind foot : *gel.*, gelatinous mass between the phalanges.
 B. The same of the front foot.

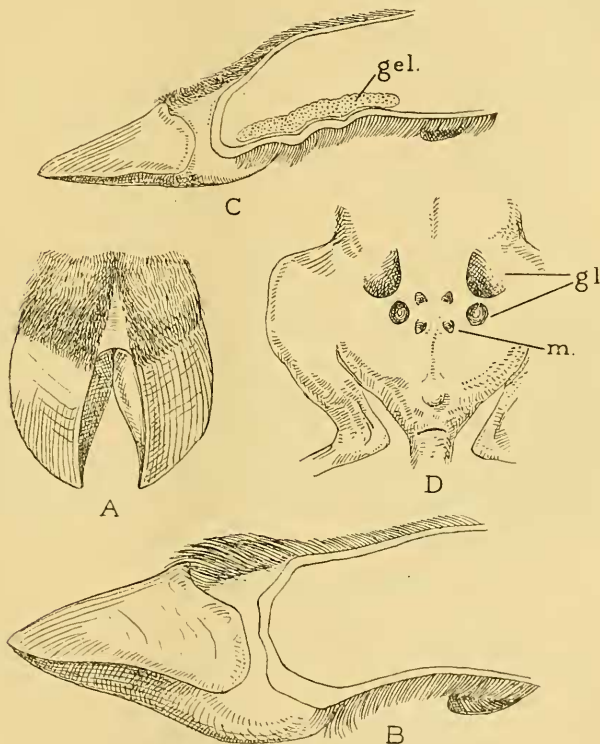
This specimen proves that Owen's statement about the inguinal glands and Ogilby's statement, apparently copied by Blanford, about the pedal glands are alike erroneous. It further shows that the prevalent view as to the kinship between *Boselaphus* and the African Tragelaphines is correct, and affords no support whatever to the suggestion found in Max Weber's 'Säugethiere,' pp. 675-676, that *Boselaphus* probably belongs to the Bubalinae and not to the Tragelaphinae.

Genus *TRAGELAPHUS* Blainv.*TRAGELAPHUS SCRIPTUS* and its subspecies.

(Text-figs. 116, C, p. 922, & 122, C, D.)

Owen records the absence of preorbital and the presence of inguinal glands in specimens of the genus he identified as *Antilope scripta* and *A. sylvatica*. W. L. Sclater, however, says that the preorbital gland is "present, but small and with a very small aperture," in the genus *Tragelaphus*, with which *Limnotragus* was included.

Text-fig. 122.



- A. Anterior aspect of foot of young specimen of *Taurotragus oryx*.
 B. Median vertical section of foot (? front or hind) of adult female of *Taurotragus oryx* (dried).
 C. Median vertical section of front foot of *Tragelaphus scriptus* ? *roualcyni*: *gel.*, gelatinous mass between the phalanges (dried).
 D. Inguinal region of female foetal example of *Tragelaphus scriptus* (subsp.?) from Unyoro; *gl.*, the two inguinal pouches; *m.*, mammae.

The only entire specimen of this genus that I have examined was a female foetal example, of which I do not know the subspecies,

from Unyoro in Uganda, which was preserved in spirit and kindly given to me by Dr. Cuthbert Christy, F.Z.S. It had no preorbital glands, but two pairs of well-developed inguinal glands resembling those of *Cervicapra redunca*, the pockets of the anterior pair being shallow but wide-mouthed, and those of the posterior pair deeper with circular orifice somewhat less in diameter than the diameter of the pocket itself. Between the orifices of the inguinal pockets were the two pairs of teats. The early development of the inguinal glands is a fact of considerable interest.

There was no trace of pedal glands and only a very shallow and short depression on the anterior surface of the fetlock close to the base of the hoofs. The interungual area was naked as in *Taurotragus*, and the web was deep, extending from near the proximal end of the front of the hoof to the heels.

I have also examined the head, feet, and skin of the inguinal region of a young male of *T. scriptus scriptus* from French Guinea, presented to the Society by Mr. Fenwick Owen. This material was preserved in alcohol. The feet were constructed as above described, and there was no preorbital gland. There were two pairs of teats, but only a single pair of inguinal glands, each consisting of a pouch about an inch deep opening by an orifice some distance away from, and in front of, the mammae of the anterior pair (text-fig. 116, C, p. 922). I think it probable that these glands correspond to the deep posterior pair, and not to the shallow anterior pair observed in the foetal example above described.

I also received from Mr. E. Gerrard the dried front and hind feet of a Bushbuck, probably belonging to *T. scriptus roualeyni*, which also had no trace of pedal glands; but in which I was able to discover the shrivelled remains of the vascular gelatinous (fatty) mass lying along the back of the pastern between the true and false hoofs, which has been already described in *Cervicapra redunca* and *Adenote kob*.

TRAGELAPHUS ANGASII Angas.

(The Inyala.)

Of this species I received from Messrs. Rowland Ward, Ltd., a single dried foot of a male, which differed in no important respects from the foot of *T. scriptus*, except that the naked shallow depression at the base of the hoofs on the front of the pastern was obliterated and the hoofs themselves were shorter with higher heels, suggesting the habit of walking on firmer ground.

Genus LIMNOTRAGUS Sel. & Poc.

LIMNOTRAGUS GRATUS Sel.

As stated above, W. L. Schater says the preorbital gland is present in the southern race of *L. gratus*, namely, *L. gratus selousi* Roths., the true Sitatunga.

I have examined no dead examples of this genus in a fresh state, but examples of the typical *L. gratus* and of *L. gratus selousi* living in the Gardens show no trace of a preorbital gland, nor of pedal glands, the widely splayed hoofs making observation of the absence of the pedal glands comparatively easy. The feet appear to resemble those of *Tragelaphus*, apart from the length of the hoofs and the nakedness of the back of the pasterns. Max Weber (Die Säug. p. 35, fig. 31, 1904) has figured the inguinal region of a male and female of *L. gratus*, showing the presence of four mammae and of a single pair of small, almost aborted, inguinal sacs, with orifices remote from and well in advance of the anterior mammae. These obviously represent the larger inguinal sacs seen in the specimen of *Tragelaphus scriptus scriptus* above described. It may further be noted that the glands as figured by Weber closely resemble in size and position the single minute inguinal sac seen on one side in the young example of *Adenota kob* (p. 916): both are suggestive of a larger sac in process of suppression.

Genus STREPSICEROS H. Sm.

STREPSICEROS STREPSICEROS Pall.

(The Greater Kudu.)

According to Owen, this species has inguinal pits but no preorbital gland. Ogilby agrees with Owen as regards the absence of preorbital glands and the presence of inguinal glands, and adds that pedal glands are also absent. He also records the presence of four mammae. W. L. Sclater, however, says that the preorbital gland and its orifice are small. I have examined no example of this species, but the available data suggest that *Strepsiceros* resembles *Tragelaphus* or *Limnotragus* in the matter of cutaneous glands, as it is well known to do in most other structural characters, apart from the slight difference exhibited in the structure of the horns. It is impossible, however, to guess whether this genus has inguinal glands like those of the foetal *T. scriptus* (subsp.?) or the young *T. s. scriptus*, described above, or like those of *Limnotragus gratus* figured by Max Weber. I suspect, however, that they will prove to resemble in size and number those of *T. s. scriptus*.

Genus BOOCERCUS, Thos.

BOOCERCUS EURYCEROS Ogilby.

(The Bongo.)

In an old skin of this species which Mr. Gerrard allowed me to examine, I found the feet to be constructed as in *Taurotragus*, there being no trace of glands and the interungual web being naked throughout its extent. I could detect no trace of inguinal glands, but found two pairs of teats.

The apparent absence of inguinal glands in this genus and in

Taurotragus and their presence in *Tragelaphus* and, as is alleged, in *Strepsiceros* are quite in accordance with the view that *Boocercus* and *Taurotragus* are more nearly allied to one another than either is to *Strepsiceros* or *Tragelaphus*, a view supported by the terminally tufted tail and the presence of horns in the female in the two former genera.

Genus TAUROTRAGUS Wagn.

TAUROTRAGUS ORYX Pall. (The Eland.)

(Text-fig. 122, A, B, p. 929.)

This species, according to Owen, who quotes it as *oreas* and *canna*, has neither preorbital nor inguinal pits. W. L. Slater, however, says that the preorbital gland is small, "with a very small circular opening in front of the eye in a narrow bare triangular space." In two young male examples examined by me, I could find no trace of preorbital gland or of inguinal or pedal glands. The pedal glands were also entirely absent on a foot of an adult kindly supplied to me by Messrs. Rowland Ward, Ltd.

The feet are constructed as in the genus *Bos*, the entire interungual area being naked, the integument that joins the hoofs together forming a deep "web" extending forwards from the heels where it is thickest, to the anterior portion of the pastern only a short distance above the proximal margin of the front of the hoof, so that the hoofs are susceptible of but little separation.

By their glands and other external features the genera of this section may be grouped and contrasted as follows:—

- a. A well-developed preorbital gland opening by a longitudinal valvular slit; horns short, not spirally twisted, present only in the male (tail not terminally tufted; no inguinal glands).
- b. Preorbital gland relatively large; horn not crested; a pouch-like gland in each false hoof of the hind leg, &c. *Tetracerus*.
- b'. Preorbital gland relatively small; horns crested basally; skin between posterior false hoofs highly glandular *Boselaphus*.
- a'. No preorbital gland; horns longish, spirally twisted.
- c. Inguinal glands present; tail hairy throughout; no horns in female *Tragelaphus*, *Limnotragus*, *Strepsiceros*.
- c'. No inguinal glands; tail terminally tufted; horns present in both sexes *Boocercus*, *Taurotragus*.

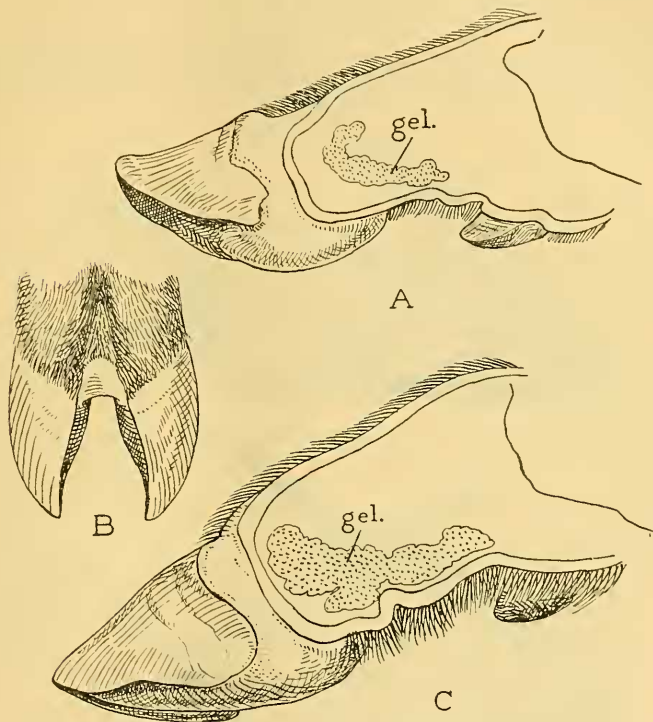
Subfamily BOVINÆ.

Genus *Bos* Linn. (Text-figs. 123, 124.)

It is agreed on all hands that preorbital, inguinal, and pedal glands are absent, and that two pairs of mammae are present in all the species of Bovinae, whether they be referred to the one genus *Bos* or the several genera *Bos*, *Bibos*, *Poephagus*, &c. In these respects Cattle are indistinguishable from the large Tragelaphine Antelopes *Taurotragus* and *Boocercus* and from the larger forms of Cervicaprine like *Kobus ellipsyprymnus*. They also resemble them in the structure of the feet, the interungual

membrane being naked and continued straight backwards from a point near the anterior proximal edge of the hoof to the heels, forming a rectangular continuation on the middle line in front and behind with the integument of the anterior and posterior surfaces of the pastern respectively.

Text-fig. 123.



- A. Median vertical section of foot of *Bos sondaicus*, three days old: *gel.*, gelatinous mass between the phalanges.
 B. Anterior aspect of the same foot.
 C. Median vertical section of foot of calf of *Bos taurus*: *gel.*, gelatinous mass between the phalanges.

I have verified this fact upon feet of specimens of the following species:—

Bos taurus L. (Ox); fore and hind feet of a calf given to me by Mr. R. E. Holding.

Bos indicus L. (Zebu); feet of adult male that died in the Gardens.

Bos frontalis Lambert (Gayal); ditto.

Bos gaurus H. Sm. (Gaur); foot given to me by Mr. R. E. Holding.

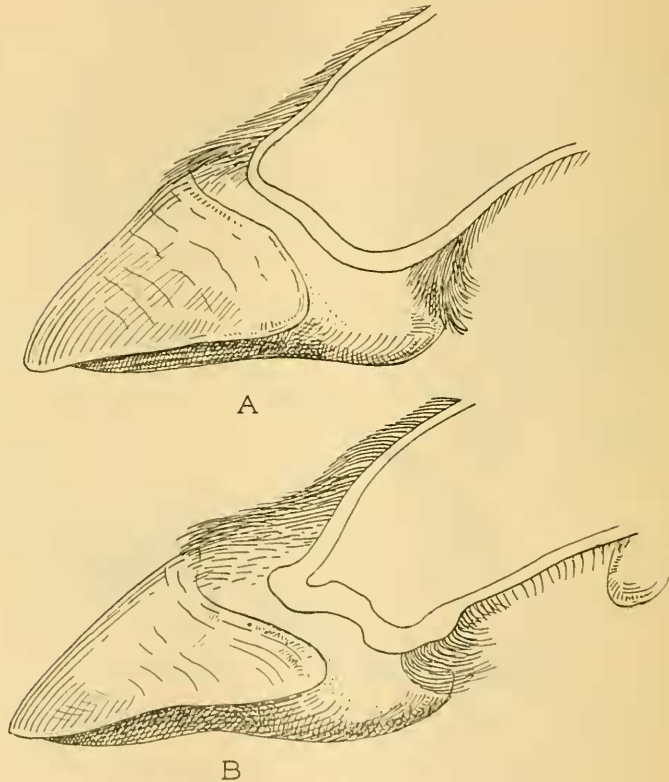
Bos sondaicus Schleg. & Müll. (Banting); calf four days old that died in the Gardens.

Bos grunniens (Yak); a female specimen.

Bos caffer Sparrm. (African Buffalo); dried foot lent to me by Rowland Ward, Ltd.

Bos bubalus L. (Indian Buffalo); ditto.

Text-fig. 124.



A. Median vertical section of foot of *Bos bubalus* (dried).
B. The same of *Bos caffer* (dried).

In fresh specimens there is always a mass of vascular gelatinous tissue between the penultimate phalanges of the pastern, corresponding to that which is found along the posterior inner surface of the pastern in fresh specimens of *Adenota kob*, *Cervicapra redunca*, *Taurotragus*, *Boselaphus*, etc.

In the feet of the two Buffaloes mentioned above I found the interdigital integument much thicker in *B. caffer* than in *B. bubalus*, and the former had a deeper depression on the front

of the fetlock above the hoofs than the latter, the interungual web not extending so far to the front and allowing the hoofs to be rather more widely spread.

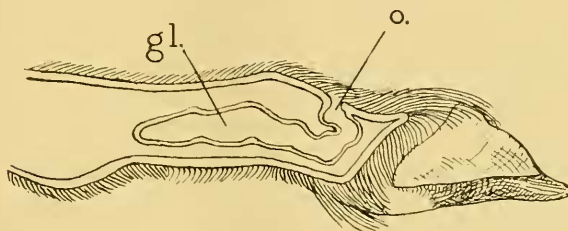
Family ANTILOCAPRIDÆ.

ANTILOCAPRA AMERICANA Ord. (The Prongbuck.)

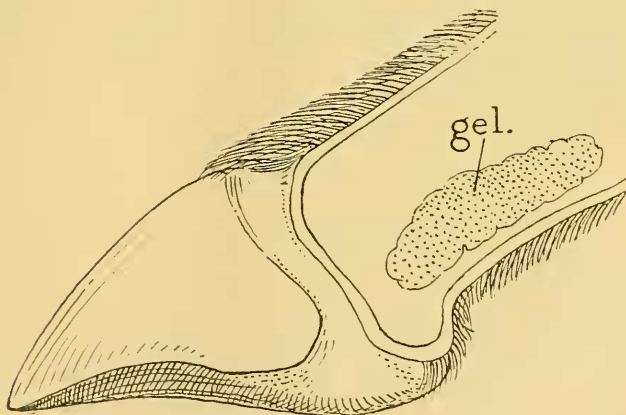
(Text-fig. 125, A.)

In his paper upon the anatomy of this species (P. Z. S. 1870, p. 340), Dr. Murie summarised his own observations and those

Text-fig. 125.



A



B

A. Median vertical section of front foot of prematurely born example of *Antilocapra americana*; *gl.*, pedal gland; *o.*, its orifice.

B. Median vertical section of hind foot of *Giraffa camelopardalis*, three weeks old; *gel.*, gelatinous mass between the phalanges.

of previous authors on the cutaneous glands as follows:—(1) no preorbital or inguinal glands; (2) a gland an inch and a half

below the ear which exudes a yellow glutinous secretion with a strong goatly odour; (3) an unpaired dorsal gland six or eight inches in front of the tail; (4) a gland on each side of the tail above the ischiatic prominence; (5) a gland on the posterior aspect of each hock; (6) interdigital glands on all four limbs.

My observations on this species were limited to a prematurely born fœtus. On this I could find no trace of the glands below the ears or on the hocks or on the ischia, except for the crease of skin at the root of the tail on each side. The dorsal gland was in a rudimentary condition, the hairs on each side of the spine of the lumbo-sacral area showing a black spot and being slightly stuck together.

In view of the absence or rudimentary condition of the glands mentioned, it was interesting to find the pedal glands highly developed. They opened by a small circular orifice on the front of the pastern some distance above the base of the hoofs. The orifice led into a long and spacious gland directed at first downwards towards the hoofs, then sharply curved upwards along the posterior wall of the pastern, occupying almost the entire space between the phalanges of the feet, nearly as far up as their articulation with the cannon-bone. These glands, present on all four feet, were crammed full of white cheesy secretion. They resembled on a very large scale the glands of Sheep more than the glands of any of the Bovidæ or Cervidæ, although the orifice was situated higher up the pastern than in *Oris*, recalling in this particular the orifice of such a Deer as *Capreolus*. It was noticeable, too, that there was no depression on the front of the pastern for the orifice to open upon. The hoofs were united by a very deep and continuously hairy web, extending from the heels as far forwards as the anterior proximal margin of the hoofs.

Family GIRAFFIDÆ.

GIRAFFA CAMELOPARDALIS Linn. (The Giraffe.)

(Text-fig. 125, B.)

According to Ogilby, the Giraffe has neither preorbital nor inguinal glands, but has small interdigital fossæ and four mammae.

A young specimen, three weeks old, that died in the Zoological Gardens, presented the characters mentioned by Ogilby except that there was no trace of "interdigital fossæ," the feet being completely webbed, with low heels and no trace of a depression on the front of the pastern. The interungual integument, moreover, was quite naked from front to back, as in Bovine and Tragelaphine Ruminants, and the same gelatinous mass of tissue was present between the penultimate phalanges of the pastern as is found in the latter animals.

There was a thick pad of hairs over and below the knees; but I could detect no evidence of glandular activity in the underlying skin, there being plenty of underwool but no secretion at the base

of the long hairs of the pad. The same pad, I noticed, was well developed in a fetal Giraffe taken from its mother that died some four years ago in the Gardens (see F. E. Beddard, P. Z. S. 1906, ii. p. 630, fig. 109).

The horns of the three weeks old specimen, which were relatively as large as in the adult, had no connection, apart from contact, with the skull, a fact already recorded by Sir Ray Lankester (P. Z. S. 1907, p. 101).

Family MOSCHIDÆ.

MOSCHUS MOSCHIFERUS Linn. (The Musk-Deer.)

(Text-fig. 126.)

The peculiar musk-gland of the male of this species has been described by many authors, and I have nothing to add to what has already been said of this organ*. Ogilby and Hodgson state that the preorbital and pedal glands are absent. Flower† confirms this, saying "nor were there any interdigital glands on either feet, the depressed space between the toes, where the glands usually open, being covered with hair." Brandt also described a gland on the outer side of the thigh in the male‡; and Hodgson discovered a gland opening on each side of the tail in that sex§. Neither the femoral nor caudal glands were found by Flower in the female example dissected by him.

I have only seen one example of this species, a male from Chamba presented to the Society by Major G. S. Rodon, F.Z.S.; at the time of its death I merely noted the structure of the feet and the absence of the preorbital gland. On the front feet it was very obvious that the long hairs of the interdigital depression were stuck together with a brown sticky substance, having a decided but indescribable smell and indicating considerable activity of the sebaceous glands. On the hind feet there was no such secretion, the hairs being clean and separable. The depression between the phalanges of the feet in this species is deep, the integument of the upper and under sides meeting at an acute angle to form a web which extends nearly as far as the heels of the hoofs; but on the hind feet the webbing is wider and not so thick as on the front feet, so that the hoofs of the former are capable of being rather more widely distended. The entire interdigital and interungual area is thickly covered with long hairs the tips of which overlap the proximal portion of the hoofs to a considerable extent.

On the dried skin I find no trace of the femoral gland described

* The scent of the secretion of this gland when fresh is decidedly unpleasant, with a peculiar pungent urinary odour. It bears no sort of resemblance that I can detect to the prepared "musk" of commerce. This is one of the criticisms that may be made on Mr. Beddard's perhaps satirical suggestion ("Mammalia" in the Cambridge Natural History, p. 13, 1902) that the musky scent of this Deer may be mimetic, in the sense of frightening its enemies by suggesting the proximity of Crocodiles.

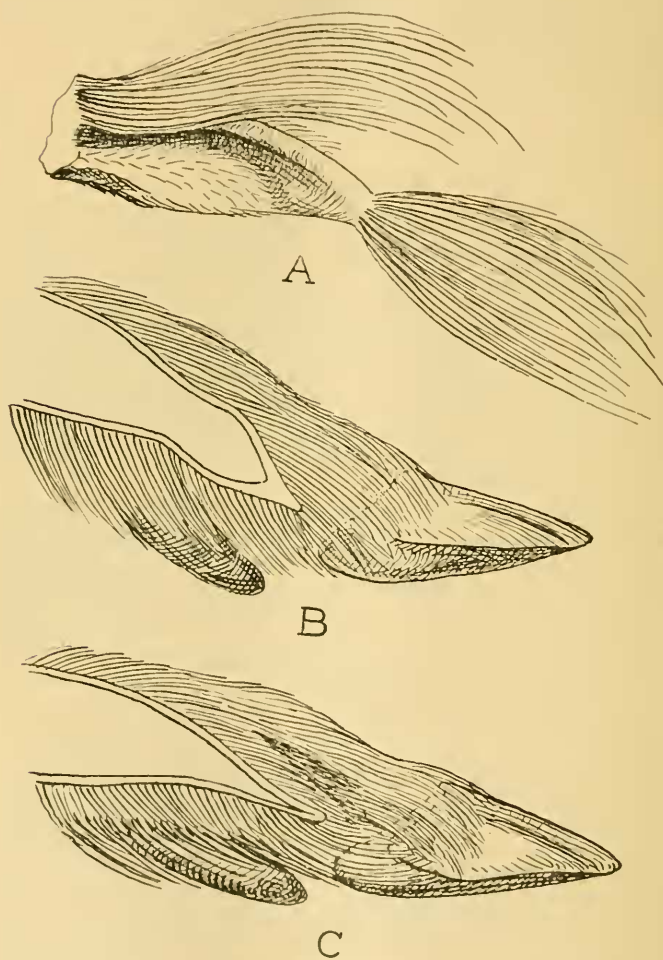
† P. Z. S. 1875, p. 159 &c.

‡ Bull. Sci. Acad. St. Pétersb. i. p. 174, 1836.

§ J. A. S. Bengal, x. p. 795, 1841.

by Brandt nor of the so-called calcic (? tarsal or metatarsal) gland mentioned by Hodgson. The tail, however, is very peculiar. It is completely buried in the long hairs of the anal region and is for

Text-fig. 126.



Moschus moschiferus ♂.

- A. Lateral aspect of tail (dried).
- B. Median vertical section of front foot (dried).
- C. The same of hind foot (dried).

the most part naked. Its tip, however, is furnished with a large tuft and its naked upper and lateral portions are overhung by long

hairs projecting backwards from its base on the upper side. Just behind the anus on the lower side there is a mat of short hairs which extends upwards laterally so as to cover the lower half of the side of the tail. Just above this the lateral surface of the tail is scooped out longitudinally, forming a wide gutter, which is filled with yellow crumbly secretion, and this extends over the summit of the tail and almost to its apex, both above and at the sides. Before the skin became shrunken with drying, it is probable that it was full and flaccid, and that the wide gutter above described had the appearance of a narrow integumental slit such as Hodgson figured.

From the great development of the caudal gland as well as of the preputial gland in the male of the Musk-Deer, it may be inferred that the females seek the males at the rutting season.

One other point may be noted: both Ogilby and Hodgson declare that this Deer has two pairs of teats. Flower, on the contrary, found only a single pair on the female he examined, and I noted that the male above mentioned also had but one pair.

Family CERVIDÆ.

In describing the cutaneous scent-glands of the Deer I have not taken into account the statements made by Fitzinger in his diagnoses of the genera of this group (SB. Akad. Wien, lxviii. pp. 348-362, 1873), because many of them are contradicted by the plainest facts. He says, for example, that *Rangifer* has no tarsal gland and that *Cervulus*, *Axis*, *Hyelaphus porcinus*, *Dorcylaphus americanus*, *Mazama nemorivagus*, and *Dama* have no pedal glands. Since these glands are extremely well developed in all these Deer, it is clear that no reliance is to be placed on this author's statements as to their absence in other species.

From the works of previous authors it is well known that one or more pairs of the following glands are present in all species of this family:—

1. Pouch-like, shallower or deeper, preorbital glands, which are apparently absent only in *Capreolus*.

2. Frontal glands, which are well developed in some species of the Muntjac group and, according to Weber, in the Sambar.

3. Tarsal glands, consisting of a hair-covered patch of thickened skin on the inner side of the tarsus or hock and especially characteristic of the American Deer.

4. Metatarsal glands, which usually resemble the last structurally, but are placed on the outer side of the metatarsus or cannon-bone of the hind leg at a varying distance below the hock.

5. Pedal glands, which when well developed consist of a large or small cleft or pouch on the front of the pastern usually of the hind foot only, more rarely of the front as well.

Inguinal glands do not exist, and there are always two pairs of teats.

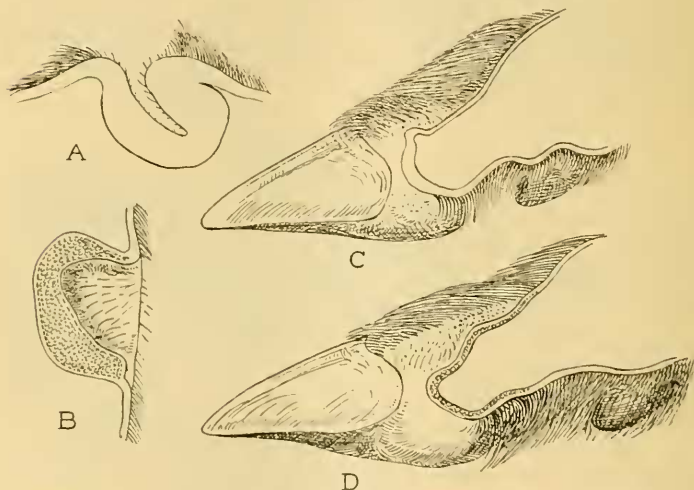
Genus *Cervus* Linn.*Cervus* (*Cervus*) *maral* Ogilby.

(The Caucasian Red Deer.) (Text-fig. 127.)

In an old Stag of this species that died in the Gardens the orifice of the preorbital gland formed a subvertical S-shaped slit at right angles to the long axis of the eye-aperture. The gland itself was a simple but deep infolding of enormously thickened skin, the pocket being scantily lined with short hair and filled with a yellow waxy secretion.

The metatarsal gland was represented by a thick mat of hair paler in colour than that of the rest of the leg. The area beneath this mat was nowhere naked, as it is in *Avis avis*.

Text-fig. 127.

*Cervus* (*Cervus*) *maral*.

A. Transverse section through preorbital gland.

B. Longitudinal section through the same.

C. Median vertical section of front foot.

D. The same of hind foot.

On the front hoof the integument of the anterior surface of the pastern formed a rather shallow depression uniformly clothed with hair almost to the bottom. The interungual integument was very thick and horny throughout its extent, forming a strong but elastic union between the hoofs. Along the back of the pastern up to the false hoofs the skin was also moderately thickened; but I could detect no evidence of any special glandular activity in the skin of the front feet.

On the hind feet the interdigital depression on the anterior side of the pastern was much deeper, the integument being much more steeply inclined backwards and downwards towards the heels, the

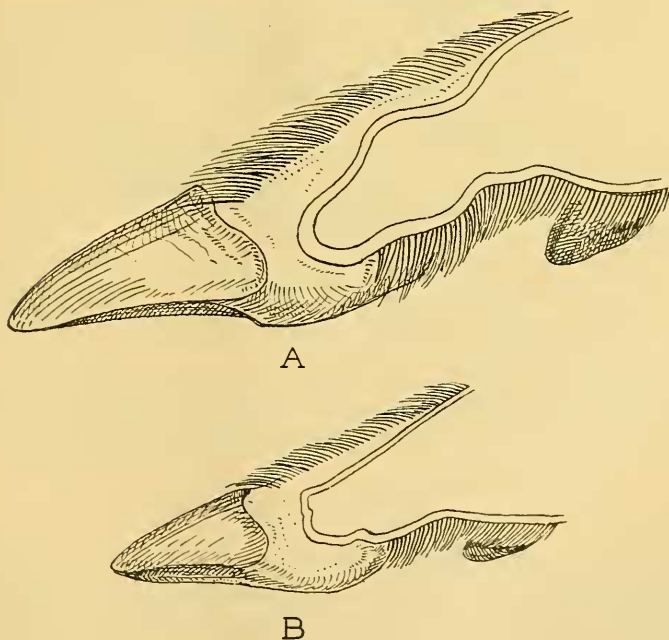
hoofs being joined together by a moderately deep and strong smooth tie just above the heels. The integument of the deeper portion of the interdigital depression was almost naked, being merely sparsely clothed with short hair, and instead of forming a continuous and level surface was sinuous or slightly folded, so that the depression was somewhat deeper above and below than in the middle. In section it was speckled with a layer of small dark spherical glands, which extended not only over the skin of the depression itself but round the interungual tie and some little distance above the heels on the back of the pastern. These dark specks, clearly visible to the naked eye, sharply define the position of the skin with active glands from the rest.

The main differences, then, between the front and hind feet are the presence of a deeper nearly naked interdigital depression, of a shorter and weaker interungual web, and of more highly developed sebaceous glands in the latter than in the former.

CERVUS (CERVUS) ELAPHUS Linn. (The Red Deer.)
(Text-fig. 128, A.)

According to Ogilby, *C. elaphus* has distinct and movable pre-orbital glands and large pedal glands. Hodgson described the

Text-fig. 128.



A. Median vertical section of hind foot of *Cervus (Cervus) elaphus*.
B. The same of *Cervus (Rucervus) duvauceli*.

preorbital glands as moderate in size and mobility and S-shaped, the pedal glands as large but doubtfully present on all four feet; and added that the metatarsal gland is posterior and external. I am indebted to Sir Claud Alexander, Bt., F.Z.S., for the front and hind feet and the mask of a freshly killed Stag from Scotland.

The preorbital gland resembled that of *C. maral*, except that the orifice, when closed, formed a long slit, lightly concave upwards and inclined obliquely at a very obtuse angle to the long axis of the aperture of the eye.

The feet also were very like those of the Caucasian species, except that the horny heels of the front hoofs were united below the strong cutaneous heel-tie and a larger area of the deep portion of the interdigital depression was very scantily clothed with short hair. On the hind foot the depression, as in *C. maral*, was considerably deeper and was divided by a transverse bridge into a smaller upper portion and a larger lower portion, both better marked than in that species.

CERVUS (CERVUS) CANADENSIS ERXL.

(The Canadian Wapiti.)

The glands of this species resemble in all essential respects those of *C. elaphus* and *C. maral*.

In an old male that died in the Gardens the orifice of the preorbital gland was inclined at an obtuse angle to the axis of the ocular aperture; the pocket was deep with nearly naked walls; the skin of the bottom at its deepest part just in front of the orbit was very thin, the thickest part being close to the orifice, especially on its anterior side. The secretion, which was very dry, smelt like green grass just beginning to decay.

The metatarsal gland consisted of thickened skin completely covered with hairs, which were white at the base and clogged with secretion smelling like a pen of Domestic Sheep.

The feet in section were very like those of *C. elaphus* and *C. maral*, except that the depression on the front of the pasterns was shallower and the nail of the hoofs shorter. The heels of the front hoofs were separated as in *C. maral*, not united as in the example of *C. elaphus* examined.

According to Hodgson, the Hangul or Cashmere Stag (*Cervus cashmirianus*), which he quotes as *C. wallichii*, and the Shou (*Cervus affinis*) agree with *C. elaphus* in their cutaneous glands.

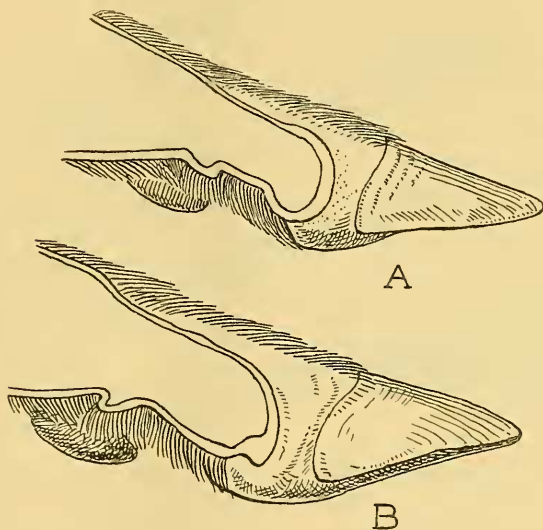
CERVUS (PSEUDAXIS) SIKA Temm. (Japanese Deer.)

(Text-fig. 129.)

Two young male examples, about eighteen months old, agreed closely in a general way with *C. maral* and *C. elaphus*, except that the preorbital glands were much less developed, the infolding being comparatively quite shallow. The metatarsal gland was marked by a large elliptical white patch, consisting for the most part of

hairs with white tips. The bases of the hairs were covered with adhesive secretion and the underlying skin was markedly thick and glandular. In both the front and the hind feet the anterior interdigital depression was naked and nearly hairless in its deeper portion, but in the hind foot it was not subdivided into an upper and a lower portion, which are so well marked in *C. elaphus*, the floor of the depression sloping gradually and evenly downwards and backwards from the tarso-metatarsal joint as in the front leg, and the interdigital web was developed to about the same extent in the two feet. In section the skin of this area showed no especial signs of glandular activity.

Text-fig. 129.

*Cervus (Pseudaxis) sika.*

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

Although, on the evidence supplied by the antlers, Mr. Garrod believed *Pseudaxis* to be nearly related to *Dama*, the structure of the feet affords no support to this view.

Pseudaxis sika readily interbreeds with *Cervus elaphus*.

CERVUS (RUCERVUS) DUVAUCELI Cuv.

(The Swamp-Deer or Bárasingha.) (Text-fig. 128, B, p. 941.)

Hodgson, who refers this species to two genera under the names *Rucervus elaphoides* vel *davauceli* and *Procervus dimorphe*, says that the preorbital glands are moderate, and moderately movable in the former, medial and vertical in the latter; that the pedal

glands are absent, and that the presence of metatarsal glands is doubtful.

In a young example, two months old, the preorbital gland was scarcely developed, and consisted of little more than a shallow naked channel running obliquely downwards and forwards from the corner of the eye. There was no trace of metatarsal gland; nor can I detect this gland in living examples of the species.

The feet were very similar to those of the previously described species. On the front leg the skin of the anterior surface of the pastern descended somewhat abruptly downwards and backwards just above the hoofs, meeting at an acute angle the portion forming the heel-tie which extended for a longer distance in a direction parallel to the sole of the foot than in the other species. There was no naked area along the middle line of the front of the pastern; on the hind foot, however, this naked area was well marked all the way up the front of the pastern, which was but little depressed and showed no indication of being deeper above and below than in the middle. The interungual integument or web formed an obtuse angle with that of the front of the pastern and a right angle with that of its posterior surface, the heel-tie being long as in the front foot. On the posterior side of the pastern the hairs did not extend between the heels, as they did for a short distance in the case of the previously described species.

It is important to note the very slight differentiation of the preorbital gland in this young specimen, and also its smaller size in the eighteen months old examples of *C. sika* as compared with that of the adult. From these facts it may be inferred that the gland in question develops with age in these Cervidae. They are quite large, however, in newly born Muntjacs (*Cervulus*).

CERVUS (PAXOLIA) ELDI Guthr. (The Thameng or Thamin.)

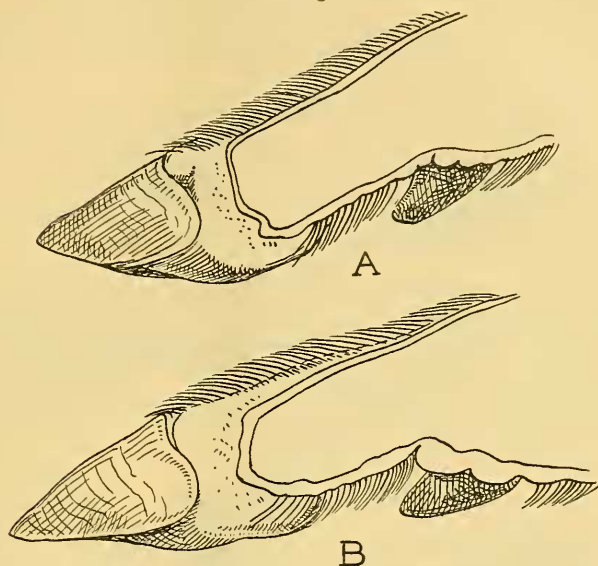
(Text-fig. 130.)

In a very old male of this species the preorbital gland was well developed, the invagination being about one inch deep at its deepest part above, the direction of the long orifice, when closed, being intermediate between that of *C. maral* and *C. elaphus*. The metatarsal gland was marked by a patch of hairs paler than those of the rest of the leg, with their bases clogged with black secretion, the underlying skin being thick and markedly glandular to the naked eye.

There was scarcely any depression on the front of the pastern of either the front or the hind foot. On the front foot the very shallow depression was hairy throughout as in *C. durauceli*, without the naked area seen in *C. maral*, *elaphus*, and *sika*; and even on the hind leg this naked area was of very small extent. Since the skin of this area did not slope downwards and backwards between the hoofs in front, it resulted that the interungual tie or web was of much greater extent than in the other species, the feet,

in section, being constructed very much as in the Tragelaphine Bovidae; but, as in the other species of Cervidae hitherto described, the interungual web was quite naked. The portion of this web which formed the heel-tie was wider than in the other Deer, giving greater distensibility to the hoofs, and the skin surrounding the false hoofs was naked, although the back of the pastern was normally hairy between the false hoofs and the heels*.

Text-fig. 130.

*Cervus (Panolia) eldi.*

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

Genus ELAPHURUS M.-Edw.

ELAPHURUS DAVIDIANUS M.-Edw.

(The Milou or Père David's Deer.)

According to Mr. Lydekker ('Deer of all Lands,' pp. 233-237) the preorbital gland is large, the metatarsal gland covered with hair and situated in the upper third of the cannon-bone, and the foot-glands and tarsal glands absent in this species.

Examination of a dried skin in the British Museum has enabled me to verify these statements, and to add to the information supplied by Mr. Lydekker the fact that the interungual integument or web is naked as in *C. elaphus*, *maral*, *sika*, *eldi*,

* In one race of this species the whole of the back of the pastern is naked as in *Limnotragus*.

and *durauceli*. Apart from the greater length of the false hoofs, the feet of *Elaphurus* seem to differ from those of the species just cited in having the integumental groove on their upper or anterior surfaces covered with short hair like that of the rest of the foot, instead of being naked at the bottom.

Opinions of authors as to the systematic position of this Deer are divided in accordance with the value attached to particular characters. Those, like Gordon Cameron and Lydekker, who rely mainly upon the antlers, place *Elaphurus* with the American Deer; Brooke, on the contrary, depending largely upon the structure of the lateral metacarpals, maintained that *Elaphurus* was an aberrant type of the group to which *C. elaphus*, *dama*, *unicolor*, and others belong.

The structure of the interdigital area of the pastern—that is to say, the absence of the glandular pouch and depression on the hind leg, and the smoothness of the interungual integument—and the high position of the metatarsal gland completely bear out Sir Victor Brooke's opinion as to the affiliation of *Elaphurus* with the Old World Deer, especially the Oriental types (*cf. infra*, pp. 969–970).

In opposition to Mr. Cameron's view that *Elaphurus* is not related to the Old World Deer, the Marquis of Hamilton ('Field,' July 1910, p. 199) pointed out that hybrids between *Elaphurus* and *Cervus* have been bred in Paris and that one of these hybrids formed fertile unions with both parent stocks at Woburn. This is an important piece of evidence in favour of relationship between the two genera.

Genus *RUSA* Ham. Smith.

RUSA UNICOLOR Bechst. (The Sambar.)

(Text-fig. 131.)

According to Ogilby, this species has distinct and movable preorbital glands and large pedal glands, the same epithets being applied to them as to those of *C. elaphus*, suggesting identity of development and structure. Hodgson supplements this description by saying that the preorbital glands are very large and completely reversile, that the pedal glands are large and present on all four feet, and that the metatarsal gland is posterior and external. According to Blanford, however, Hodgson says the interdigital glands are wanting. I have seen one old male example of this species.

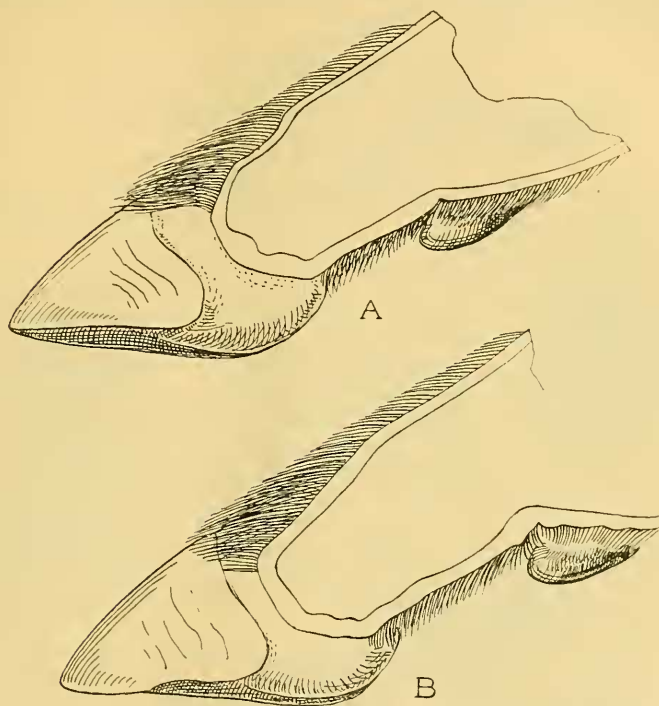
The preorbital gland was a large and deep, naked invagination half filled with a quantity of waxy secretion with a strong but indescribable odour. The integument at the bottom of the pouch was thin and apparently not glandular; but round the orifice, especially anteriorly, it was much thickened, and it was here apparently that the secreting area was concentrated.

The supraorbital gland, mentioned by Weber as present in

Rusa equina, I did not find; and no living Sambar that I have seen has any gland on the forehead comparable in development to that of the Muntjac (*Cervulus*).

The metatarsal gland was represented by a tuft of hair, which, as in *Elaphurus* and *Cervus*, completely covered the underlying skin. No evidence, however, of the glandular activity of the skin was supplied by secretion at the base of the hairs.

Text-fig. 131.



Rusa unicolor.

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

Neither on the front nor the hind feet was there a trace of interdigital depression such as is seen in the Axis and Hog Deer. The front of the pastern in both feet was only shallowly depressed and was covered with hair as in *Elaphurus*, and the intertarsal web was quite naked as in the latter and in the typical Old World Elaphine Deer.

The difference in the structure of the hind feet between the Sambar and the Axis justifies the generic separation of the two; with this is correlated the nakedness of the metatarsal gland in

the latter animal and its hairy clothing in the former. On the other hand, although the Sambar resembles the Bárasingha (*C. (Rucereus) duvauceli*), the Thamin (*C. (Panolia) eldi*), and the Japanese Deer (*C. (Pseudaxis) sika*) in the structure of the feet, it may be generically distinguished from these as well as from the typical Elaphine Stags by the longer bushier tail and the extension of the muffle as a distinct broadish rim of moist hairless skin beneath the nostril.

According to the Marquis of Hamilton this species interbreeds with *Cervus elaphus* ('Field,' July 1910, p. 199).

Genus *Axis* Ham. Smith.

Axis (*Axis*) *axis* Erxl. (The Chital or Spotted Deer.)

(Text-fig. 132, A-E.)

Hodgson says that the preorbital glands are large and very movable, the pedal glands large and present only in the hind feet, and that the metatarsal gland is posterior and external. This is perfectly correct, according to my observations.

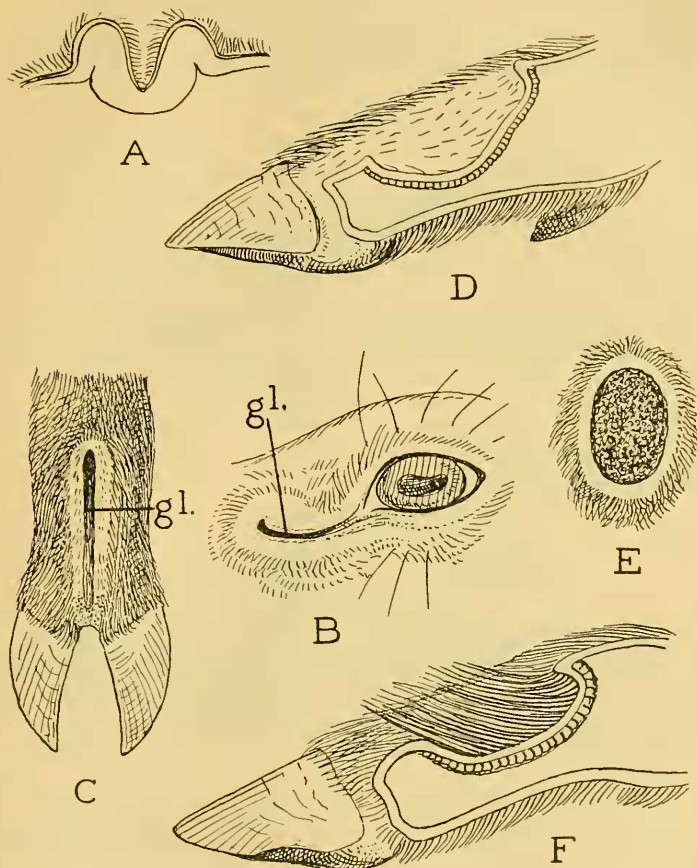
In an old male that died in the Gardens, the infolding of the preorbital gland was decidedly shallower relatively to the size of the animal than in *C. mural*, or *C. elaphus*, or *C. eldi*, and the line of the orifice, when closed, was nearly parallel to that of the long axis of the aperture of the eye and lightly concave upwards. The pocket was lined with hair of the same colour as that of the face. By squeezing, the gland could be made to yield drops of pale moisture with a faint but decided musky smell.

The metatarsal gland was represented by a horny, hairless, blackish oval patch of skin, exactly like the wart of a Zebra or Wild Donkey and surrounded by a narrow rim of pale naked skin. This patch was entirely concealed by the long hairs growing immediately round it, recalling in this respect the metatarsal gland of the Impala (*Ephyrceros*).

On the front feet there was only a very shallow depression on the anterior surface of the pastern; but on the hind feet the pedal gland was well developed and represented by a long and deep depression starting at the top of the pastern and extending almost to the hoofs. At its deepest part the wall of the depression almost reached the skin of the posterior surface of the pastern. From this point it gradually shallowed above and below. Its upper edge reached the summit of the pastern, but its lower edge was sunk some distance below and above the proximal portion of the hoof, where it was continued into the interungual tie, which extended backwards from near the middle of the hoof to the heels, equalling in depth the corresponding web or tie of *Cervus mural* and *elaphus*. As in those species this tie was naked, the hairs beginning just between the heels and being continued up the back of the pastern. From the above-given description it may be inferred that the skin forming the lower rim of the inter-

digital depression is separated by a considerable space from the skin of the inferior part of the back of the pastern above the heels and that the interdigital depression, instead of communicating freely with the space between the hoofs, is to a great extent shut

Text-fig. 132.



- A. Transverse section of preorbital gland of *Axis* (*Axis*) *axis*.
 B. Part of the face of the same showing eye and gland (*gl.*).
 C. Anterior aspect of hind foot of same: *gl.*, slit-like orifice of gland.
 D. Median vertical section of the hind foot of the same.
 E. Metatarsal gland of the same with the hairs pulled aside to show naked skin.
 F. Median vertical section of hind foot of *Axis* (*Hyalaphus*) *porcinus*.

off from it by the deep interungual tie. The walls of the depression were scantily clothed with quite short hairs stuck

together and stained with brownish secretion, and the layer of secreting cells was restricted to the walls of the interdigital depression and were much more highly developed than in *Cervus maral*.

AXIS (HYELAPHIUS) PORCINUS Zimm. (The Hog-Deer.)
(Text-fig. 132, F.)

According to Hodgson, the Hog-Deer agrees with the Axis in the development and structure of its cutaneous glands, both species being referred to the genus *Axis*.

In a general way, this was true of the one example, an adult female, which I examined in a fresh state. The invagination of the preorbital gland was, however, shallower than in the male Axis. The pedal gland differed, too, in one interesting particular. Its walls were covered with a growth of long hairs projecting forwards from the orifice of the depression exactly as in the Bubaline Antelopes. These hairs were clogged basally and stained yellow by a waxy secretion with a pungent but indescribable smell. Moreover, the interungual skin of the hind foot was hairy; of the front foot it was naked, recalling what occurs in the Muntjac. The naked metatarsal patch was overlapped by the long marginal hairs as in *A. axis*.

I have seen hybrids between the Chital and the Hog-Deer in the possession of Sir Claud Alexander, by whom they were bred.

Genus DAMA Frisch.

DAMA DAMA Linn. (The Fallow-Deer.)
(Text-fig. 133.)

The structure of the feet and of the pedal glands of this Deer have been described accurately by Max Tempel. The material I have examined were a fawn about 24 hours old received from Mr. R. E. Holding, some hind feet purchased in a shop in London, and preparations of the feet in the Museum of the Royal College of Surgeons.

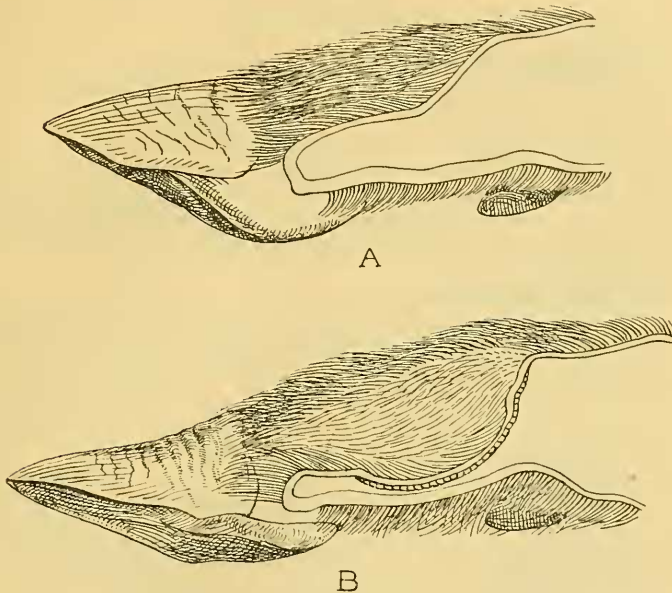
In the fawn the preorbital gland consisted of a small but very distinct pit of naked skin. This pit was considerably deeper relatively than in the much older young example of *Cervus (Rucervus) duvauceli*, but was shallower than in the fawn of *Cervulus muntjac*.

The area of the metatarsal gland was quite covered with long white close-set hair; but the gland showed no signs of activity.

The cleft of the pedal gland of the hind foot was as long as in *Axis axis* or *A. porcinus*; but the cleft itself was decidedly deeper, the skin of the posterior wall being almost in contact with that of the back wall of the pastern. As in *A. axis* the deepest part of the depression was at a point nearly midway between the heels and the false hoofs; above the deepest part the skin sloped

somewhat steeply upwards to the joint of the pastern, but below it the skin rose to only a very slight extent before passing into the heel-tie, with which it formed a close fold. Thus the interdigital cleft communicated quite freely with the space between the hoofs and was not shut off therefrom by any extension of the integument to form an interungual tie or web. The hoofs were united only at the heels; but by way of compensation for this shallow junctional area the heel-tie was very thick and horny. It was naked behind. The whole of the interdigital cleft was thickly

Text-fig. 133.



Dama dama.

- A. Median vertical section of front foot, from specimen in the Museum of the Royal College of Surgeons.
B. Median vertical section of hind foot.

clothed with hairs, growing for the most part downwards and grey or white in colour, but stained a deep yellow and stuck together basally with secretion. Inferiorly these hairs spread over the lower rim of the orifice formed by the closely folded skin above the heel-tie. The hair along the back of the pastern spread for a short distance between the heels, and the secreting cells of the gland were restricted to the walls of the interdigital cleft.

In the Museum of the Royal College of Surgeons there are preparations of the feet of this Deer. The hind foot agrees with

the one above described, and the front foot shows a very deep cleft similar to that on the hind foot but shallower, the web of the heel-tie being much less closely folded.

Although, in the opinion of some authors, *Dama* is merely a sub-genus of *Cervus*, the structure of the feet shows that it must rank as quite a distinct genus from all Elaphine Deer to which it is commonly supposed to be nearly allied. The only Deer, so far as my knowledge extends, which have the hind feet so deeply cleft are the Muntjacs (*Cervulus*) and the Chinese Water-Deer (*Hydropotes*).

I am not aware that the Fallow-Deer ever interbreeds with the Red Deer.

Genus CERVULUS Blainv.

CERVULUS MUNTJAC Zimm. (The Common Indian Muntjac.)
(Text-fig. 134.)

According to Ogilby, this species has very large movable pre-orbital glands, two large movable supraorbital glands at the base of the horns, and large pedal glands. Hodgson confirms what Ogilby says about the preorbital and supraorbital glands, and adds that the pedal glands are confined to the hind feet and that the metatarsal gland is absent.

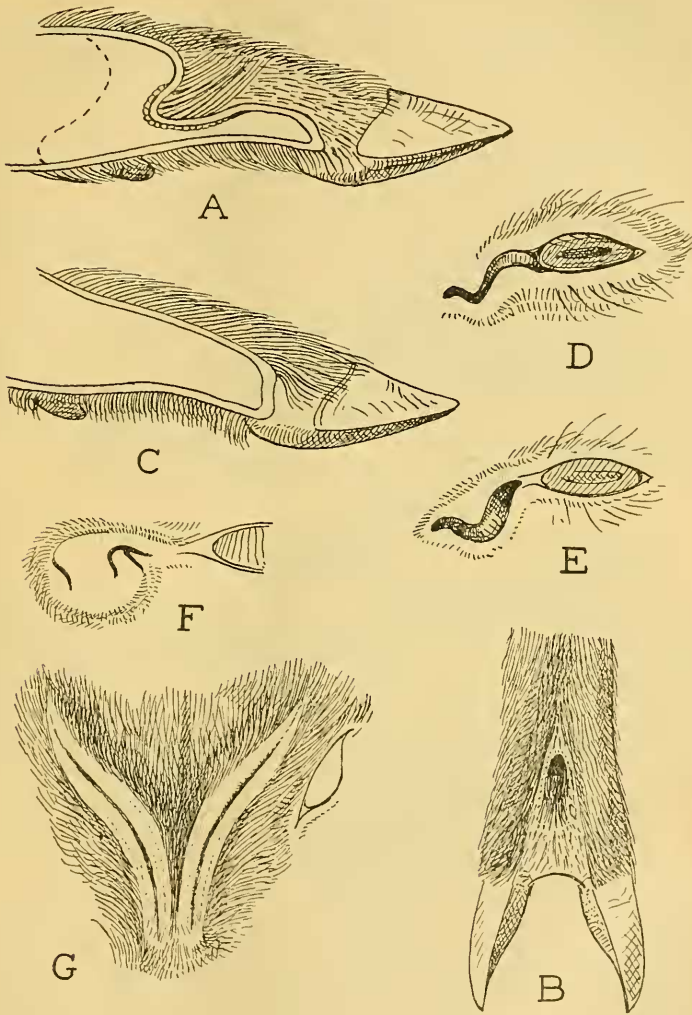
My own observations upon a specimen six days old that died in the Gardens, agreed precisely with those of Hodgson. The frontal gland was represented by two anteriorly converging strips of skin covered with very short hair, and shallowly grooved or rather longitudinally depressed along the middle line. This area of skin was in no sense thickened, and in section showed no macroscopic indication of being specially glandular. This was probably attributable to the immaturity of the specimen, for in living adult examples of this species now living in the Gardens this gland appears as a long crease with thickened upstanding edges, and, be it noted, it is much better developed in the male than in the female.

The preorbital gland when closed has the form in the adult of a crescentic slit with the concavity directed upwards. The posterior extremity of the slit, however, curves back towards the shallow groove running forwards from the eye, and its opposite extremity curves slightly the other way, giving in reality a slightly sigmoid curve to the slit. The two ends of the slit are deeper than its median portion, and when the gland was everted in the young individual its area was seen to be subcircular and marked with an anterior and posterior groove representing the deeper parts of the slit.

There was no trace of tarsal or metatarsal glands or tufts of hair; and the pedal glands were present only on the hind feet, the front of the pastern bearing a deep triangular cleft when the hoofs were separated. The skin of the back of the pastern reached the heels, and was folded somewhat closely back upon

itself, though not quite so closely as in *Dama*. The anterior skin of this fold or web formed the posterior wall of the interdigital

Text-fig. 134.



Cervulus muntjac.

- A. Median vertical section of hind foot of specimen six days old.
- B. Anterior aspect of hind foot of the same.
- C. Median vertical section of front foot of the same.
- D, E, F. Preorbital gland, in three stages of distension, of the same.
- G. Frontal glandular areas of the same.

cleft, the upper portion of which was depressed to form a shallow pocket with a narrow elongated orifice, whence long hairs, stuck together with secretion, projected. This pocket was the glandular area of the cleft. The sides of the cleft were covered with hair, as also was the interdigital web.

On the front foot the skin of the anterior surface of the pastern formed a very slight and gradual slope between the digits until it reached a point on a level with the heels, whence it receded somewhat abruptly, forming a moderately deep interungual web, which met the skin of the back of the pastern at right angles, constituting the heel-tie. In this foot the heel-tie and interungual web were smooth and not hairy as in the hind foot.

In a young male of about a year old examined since the one just mentioned was described, I found the glands similarly but better developed. For instance, the dark glandular layer of the pedal glands was much thicker, and the white hairs of the depression were stained a rich grass-green colour by the secretion, the smell of which might be described as "musteline," being decidedly unpleasant and reminding me of the scent of a Skunk (*Mephitis*). When the frontal gland was excised and squeezed, minute drops of clear fluid appeared on the skin. This had quite a pleasant odour, very like that of a living Civet (*Viverra civetta*) or of the waxy substance cobblers call "heel-ball."

CERVULUS REEVESI Ogilby. (Reeves' Muntjac.)

(Text-fig. 135, E.)

I had an opportunity of examining the glands on a fresh nearly adult female specimen of this species sent to the Gardens by Mr. W. Jamrach for determination. The frontal glands were not nearly so well developed as in *C. muntjac*: in the latter the nearly naked areas of skin converge and meet on the summit of the nose; but in the specimen of *C. reevesi* examined they were considerably shorter, subparallel, and separated throughout their extent by a normally hairy area of skin.

The preorbital glands were of substantially the same structure in the two. The secretion was white and adhesive, with a strong smell of cream-cheese.

The interdigital cleft of the hind foot had no differentiated glandular pocket in its upper half, but was evenly deep throughout its length, very closely resembling that of *Dama dama*, the interdigital web consisting of a close fold of skin running along the back of the lower half of the pastern and tying the heels together where the fold began. This heel-tie and the walls of the cleft were covered with hairs, and long hairs projected forwards and downwards from its deeper portion, exactly as in the Hog-Deer (*Axis porcinus*).

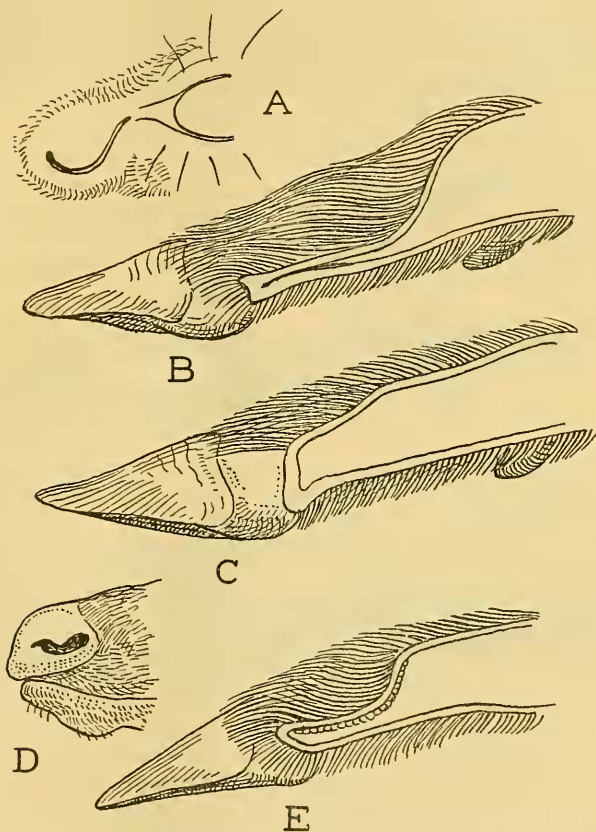
Genus ELAPHODUS M.-Edw.

ELAPHODUS CEPHALOPIUS or MICHIANUS.

(The Chinese Tufted Muntjac.) (Text-fig. 135, A-D.)

In his memoir on the anatomy of *E. michianus*, Garrod does not mention the pedal glands. He records, however, the absence

Text-fig. 135.



- A. Orifice of preorbital gland and part of the eye of *Elaphodus michianus*.
 B. Median vertical section of hind foot of the same.
 C. Do. of front foot of the same.
 D. Rhinarium.
 E. Median vertical section of hind foot of *Cervulus reevesi*.

of frontal glands and the presence of preorbital glands in both sexes*.

* P. Z. S. 1876, p. 757.

I am indebted to Mr. Edward Gerrard for the opportunity of examining a dry skin of a female of one of these Deer, probably referable to the Ningpo subspecies *E. cephalophus michianus*. There was no trace of frontal gland.

The preorbital glands differed in no respects from those of *Cervulus*, consisting of a subcircular area of short-haired integument with a subcrescentic crease deeper at the two ends than in the centre. The pedal gland of the hind foot resembled that of *C. reevesi*, except that the cleft was relatively longer. On the front foot there was no gland and only a shallow depression, the interungual web being moderately deep, owing to the anterior and posterior skins of the pastern being considerably separated in the middle line. The heel-tie and interungual web were quite naked. The false hoofs were of comparatively large size and the hoofs were shorter than in *C. reevesi*.

There were two pairs of teats as in other Deer. The absence of the frontal glands and the presence of well-developed false hoofs show that *Elaphodus* is a less specialised type than *Cervulus muntjac* or *reevesi*. False hoofs, however, are by no means always absent in specimens in the Gardens referred to *C. muntjac*.

Genus HYDROPOTES Swinh. (=HYDRELAPHUS Lydd.).

HYDROPOTES INERMIS Swinh.

(The Chinese Water-Deer.)

I have seen no example of *Hydropotes* (= *Hydrelaphus* Lydd.), but, according to Garrod (P. Z. S. 1877, p. 780), the preorbital gland was present, but quite small, in a newly-born specimen of *H. inermis*, and the metatarsal gland was absent. Of the pedal glands this author wrote:—"In the fore-limb the interdigital skin is inflected but slightly, and there is no special gland differentiated, although the surface of the skin is apparently studded with minute gland-openings. In the hind-limb the interdigital skin forms a deep pocket which almost completely separates the toes, except that they are joined by a thin transverse skin-fold along their posterior edges. The included skin is studded with small glands." I infer from this description that the posterior pedal gland resembles that of *Cervulus* or *Dama* and is quite unlike the corresponding gland of *Capreolus*, the genus near which Sir Victor Brooke placed *Hydropotes* on account of the structure of its lateral metacarpals and vomer. Since W. A. Forbes came to the same conclusion touching the affinities of these two genera judging from their visceral anatomy (P. Z. S. 1882, p. 637), there is no reason to doubt the correctness of Sir V. Brooke's view. All the more interesting, therefore, is it to find the difference in the pedal glands above alluded to; because *Hydropotes* is the only member of the Telemetacarpal Deer yet recorded as having the interdigital glandular cleft communicating

freely with the interungual space as in *Dama* and *Cervulus*, this type of gland being, in my opinion, as is explained below, the most primitive type in the Ruminants.

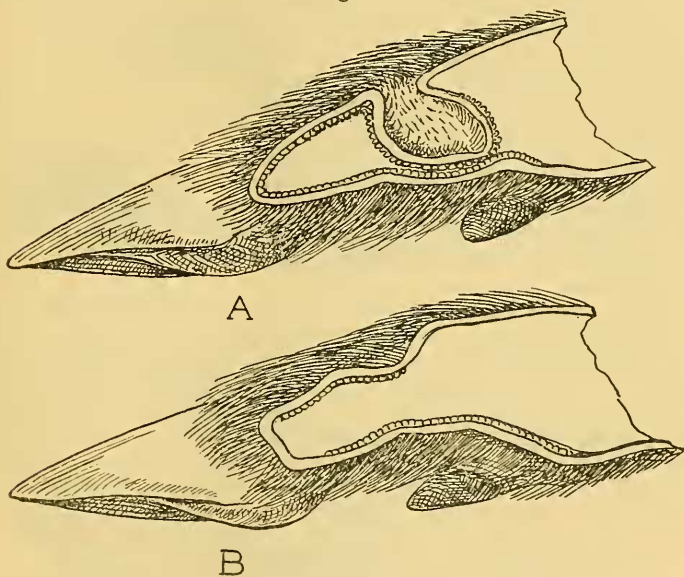
Genus *CAPREOLUS* Frisch.

CAPREOLUS CAPREOLUS Linn. (The Common Roe.)

(Text-fig. 136.)

According to Ogilby, this species has no preorbital glands, but large interdigital glands; and since he described the pedal glands both of *Cervus elaphus* and of *C. capreolus* as "*fossæ interdigitales magnæ*," it might be inferred that they have the same structure

Text-fig. 136.



Capreolus capreolus.

A. Median vertical section of hind foot. | B. Median vertical section of front foot.

in the two species. This inference, however, is as little in accord with the facts as the statement that the pedal glands of *Capreolus* are very like those of *Hydropotes* *. Max Tempel accurately figured and described the glandular structures both on the front and hind feet of *Capreolus*.

The only material of this species which I have been able to examine was some limbs of freshly killed specimens kindly

* Lydekker, 'Deer of all Lands,' p. 223.

procured for me by Dr. Plimmer, F.R.S., Pathologist to the Society, and by Mr. R. E. Holding, and a face-skin for which I was also indebted to the latter gentleman. Mr. Lydekker describes the face-gland of *Capreolus* as "almost obsolete." I could find no trace of it on the face-skin that I examined.

The metatarsal gland was represented by a thick pad of hairs, the bases of which exhibited blackish secretion derived from the thickened skin beneath. I could detect no distinct smell in connection with this gland.

The pedal gland of the hind foot was represented externally by a smallish orifice opening on the front of the pastern high above the hoofs. This constricted orifice led into a capacious sac extending as far back as the posterior skin of the pastern and also to a certain distance upwards, its upper extremity reaching as far as the false hoofs. The walls of the sac were scantily clothed with long pale hairs all stuck together with thick yellow secretion smelling like cheese. The dark brown gelatinous-looking glandular layer enveloped not only the sac itself but the skin of the front of the pastern below it and the skin of its posterior side up as far as the false hoofs. The hair between the hoofs was all matted with secretion. Below the orifice of the glandular pouch the skin of the middle line of the pastern was only slightly depressed; the anterior and posterior walls of the interungual web were moderately widely separated and in no sense closely folded as in *Cervulus* or *Dama*. This web was, however, uniformly and thickly covered, both above, below, and between the heels, with long hairs.

On the front leg the glandular sac was represented by a very shallow depression, but the skin of the pastern below this down to the hoofs and of the back of the pastern from the heels up to the false hoofs was lined with a dark secreting layer. This layer did not, however, extend up the interungual web, which was deeper than that of the hind foot but similarly hairy. The hairs both on the front and the back of the pastern were stuck together basally with blackish sticky secretion smelling of mouse urine.

Genus *ALCE* Frisch.

ALCE ALCES Linn. (The Moose.)

(Text-fig. 137.)

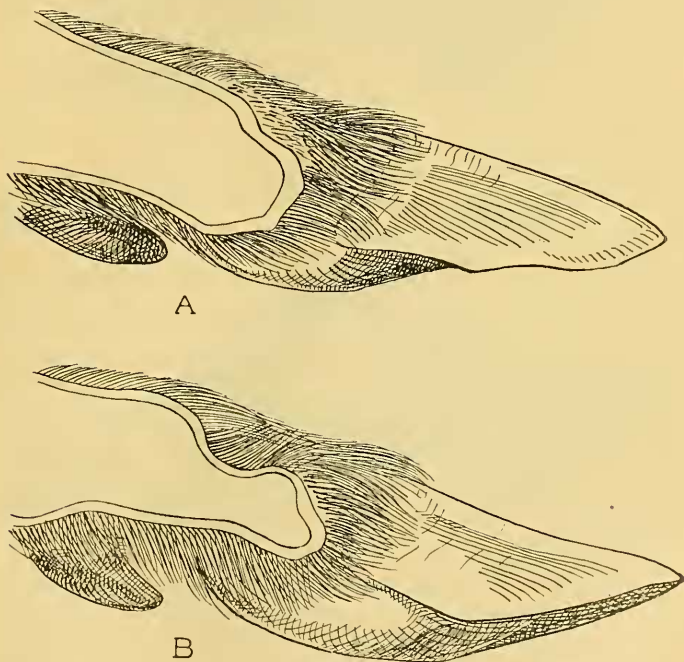
According to Ogilby, this species has large preorbital and pedal glands. Subsequent authors have also recorded the presence of preorbital, tarsal, and metatarsal glands, the latter, according to Nitsche (Zool. Anz. xiv. p. 181, 1891), being represented by a naked area of skin overlapped by a marginal fringe. Max Tempel accurately described the structure of the feet and the microscopic structure of the glandular pocket of the posterior foot.

I have nothing new to add on these points, the only material of the genus I have been able to procure for examination being

two feet which, from certain differences in their structure, I judge to be those of front and hind legs. The former I received from Mr. R. E. Holding, the latter from Messrs. Rowland Ward, Ltd.

On the one judged to be the hind foot the interdigital pocket found in *Capreolus* and *Rangifer* was represented by a distinct but shallow depression, with hairs paler than those of the surrounding skin projecting from it. A little below this the integument dipped obliquely backwards and downwards towards the heels to meet that of the posterior side of the pastern, which extended for some distance between the heels but was not markedly thickened to form a strong heel-tie. The entire interungual area and heel-tie were covered with long hairs, there being only a small less thickly haired area a little below the glandular depression.

Text-fig. 137.



Alce alces.

- A. Median vertical section of front foot (dried).
B. The same of hind foot (dried).

On the front leg there was scarcely a trace of the glandular pocket seen on the other, but the slightly depressed skin along the middle line of the front of the pastern towards the hoofs was scantily hairy, this area being of much greater extent than on the foot previously described. Moreover, the interungual web

was much thicker and deeper, the two halves of the hoof of the front foot being evidently much more strongly united than those of the hind foot. As in the latter, the whole interungual tie was thickly covered with long hairs, this hairy clothing constituting a marked difference between the feet of the Moose and those of the Red Deer group, and showing equally marked similarity between the Moose, Roebuck, Reindeer, and typical American Deer.

Genus RANGIFER Frisch.

RANGIFER TARANDUS Linn. (The Reindeer.)

(Text-fig. 138.)

According to Ogilby, this Deer has large preorbital and small pedal glands. Max Tempel shows that there is a well-developed glandular pocket on the hind foot, but none on the front foot. My own observations are completely in accord with this.

The only material of this species I have been able to examine was the fore and hind feet of the Caribou (*R. tarandus caribou*) lent to me by Mr. Gerard, and the fore foot of a second example received from Messrs. Rowland Ward, Ltd.

The tarsal gland consisted of a large area of thickened skin covered with a mat of long coarse white hairs without underwool, the bases of the hairs being clogged with colourless scurfy secretion.

The pedal gland opened by a large orifice on the front of the pastern some distance above the proximal edge of the hoof. The orifice led into a deep subcylindrical pocket, the deeper end of which extended obliquely backwards and upwards in the direction of the false hoofs. The cavity of this sac was filled with long hairs, all directed towards the orifice and stained yellow, and a well-marked dark-coloured secreting layer enveloped the walls of the sac within the pastern. The interungual web was very short, and was situated some distance from the heels towards the proximal end of the hoof in front, forming in section a semi-elliptical figure. Like the back and the front of the pastern, it was thickly covered throughout with long hair.

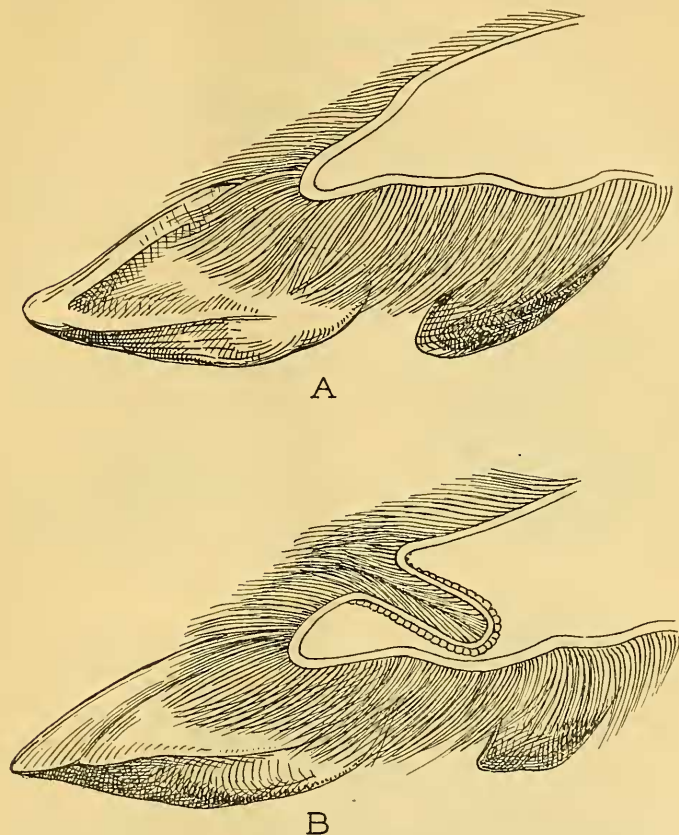
The front foot was, in a general way, like the hind foot, but had no trace of the glandular pocket, and the interungual web was even less extensive and still further removed from the heels.

The resemblances between the glands of the feet of the Reindeer and those of the Roe (*Capreolus*) or Brocket (*Mazama*) are unmistakable, and are quite in accord with Sir Victor Brooke's view of the relationship between these Deer.

Writing of the foot of the Reindeer, Flower and Lydekker remark:—"The cleft between the two main hoofs is very deep, so that these hoofs can be spread out as the animal traverses the snow-clad regions in which it dwells" ('Mammalia,' p. 325, 1891). This expression, although true in a sense, by no means conveys an accurate impression of the cause of the potential expansion of

the hoofs of this species, nor does it suggest the difference between the distensibility of the hoofs in the Reindeer and those of the Red Deer for example.

Text-fig. 138.



Rangifer tarandus.

- A. Median vertical section of front foot (dried).
B. The same of hind foot (dried).

The peculiarity of the foot of the Reindeer consists in this :— The integumental web joining the two hoofs together passes straight forwards some distance above the heels and terminates behind and nearly on a level with the upper posterior margin of the nail. From this arrangement it results that whereas the superior and proximal portions of the hoof are capable of comparatively little distension, the heels can be widely separated, giving to the hoof a wide plantar area which is increased by the long false hoofs. It is only when the hoofs are thus distended

that the plantar surface, or sole, of each is applied flat to the ground, on account of the much greater size of the external as compared with the internal lamina of the nail.

Genus DORCELAPHUS Gloger.

DORCELAPHUS (or CARIACUS) AMERICANUS Erxl.

(The Virginian Deer.) (Text-fig. 140, C, p. 965.)

I have had no dead example of this species for examination, but in the collection of the Royal College of Surgeons there are mounted specimens of the fore and hind feet showing the pedal glands. The glands on the hind foot resemble in a general way both in position and development those of the Roebuck (*Capreolus*), except that the orifice is relatively larger and less constricted. As in the other Telemetacarpal Deer that I have seen, the interungual integument is covered with longish hairs, continuous in front and behind with those of the anterior and posterior sides of the pastern respectively.

The front feet are similarly constructed, and have a large pocket-like gland resembling that of the hind feet but smaller. This is the only species of Deer known to me which has a large pedal gland on the fore foot.

The presence of preorbital, tarsal, and metatarsal glands in this and allied species has been recorded by other writers, and they are all apparent upon a living specimen in the Gardens, from Venezuela, which I identify as *D. americanus savannarum*.

Genus MAZAMA Raf.

MAZAMA NEMORIVAGUS F. Cuv. (The Wood-Brocket.)

(Text-fig. 139.)

I have examined one adult female of this species.

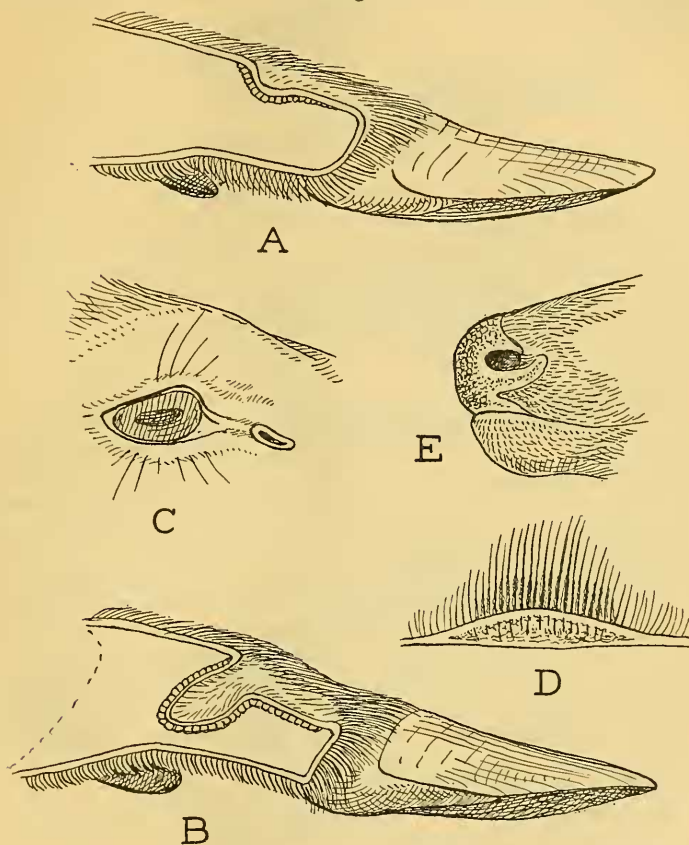
The preorbital gland was a small shallow infolding, linear when closed and subelliptical when spread, resembling that of an eighteen months old *Cervus sika*.

The hock- or tarsal gland was marked externally by a small tuft of whitish or ashy-grey hairs arranged in a whorl and with their bases encrusted with dark brown secretion, the underlying skin being thick in section, with the roots of the hairs penetrating deeply into it. There was no metatarsal gland.

The pedal gland was well developed upon the hind foot. The front of the pastern was marked by a shallow triangular depression, at the summit of which was the orifice of a cylindrical sac resembling that of the Reindeer (*Rangifer*), the deep end of the pocket reaching nearly to the false hoofs. The walls of the pocket were sparsely lined with hairs covered with secretion which stained black the longer hairs of the depression below the orifice of the gland. The secreting layer of cells enveloped the pocket and extended along the skin forming the posterior wall of

the depression down to the point where it passed into the inter-ungual web. This was deep and projected straight backwards from a point about on a level with the middle of the proximal edge of the nail nearly to the posterior part of the heels, meeting at right angles the skin of both the anterior and posterior walls of the

Text-fig. 139.



Mazama nemorivagus ♀.

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Ocular region and preorbital gland.
- D. Section of tarsal gland.
- E. Rhinarium.

pastern which were widely separated. The interungual web was uniformly covered with longish hairs barely overlapping the proximal edge of the nail. The hoofs were long and pointed.

The front hoof was constructed almost exactly like the hind,

except that the pocket was represented by a very shallow depression, and the area of the pastern below this was scarcely depressed. The secreting layer of cells lined the integument in exactly the same way.

I believe this species to have been correctly determined; yet, according to Fitzinger, *M. nemorivagus* has no tarsal gland, and was consequently made the type of that author's genus *Doryceros*.

MAZAMA BRICENII Thos. (Briceni's Brocket.)

(Text-fig. 140, A, B.)

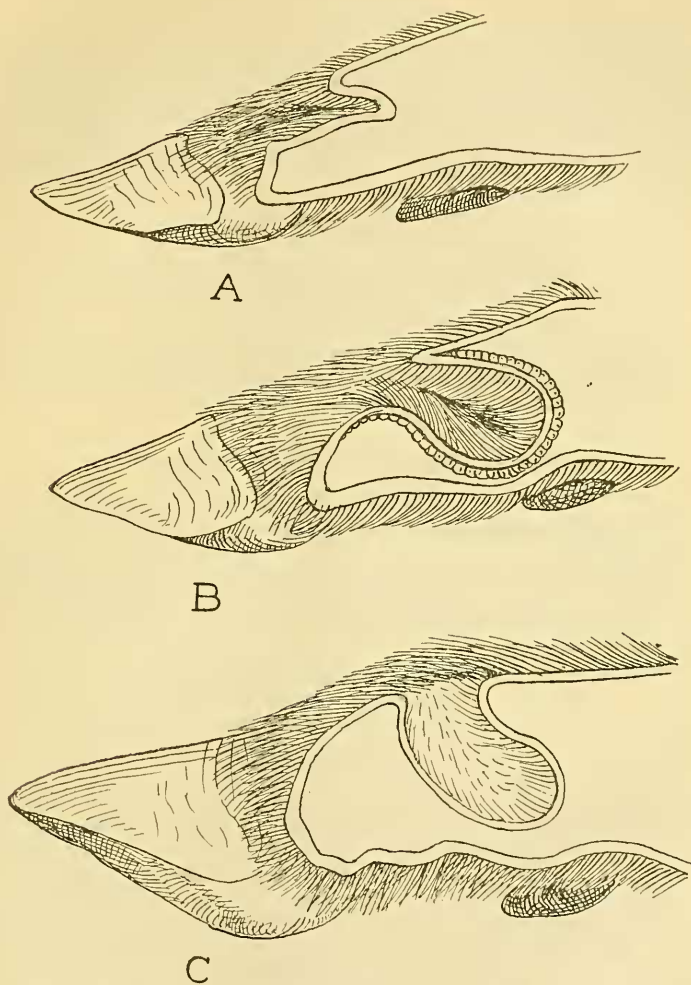
A single adult female example from Venezuela. The preorbital gland resembled that of *M. nemorivagus*. Superficial examination of the hock showed no trace of the tarsal gland, but when the hairs over the appropriate spot were rubbed aside they were seen to have darker bases than elsewhere on the leg and the underlying integument was thickened as in *M. nemorivagus* although to a much less degree. On a dried skin these glands would probably have been wholly overlooked, since they were not marked by any tuft of hairs thicker or coarser than those surrounding the area.

The feet were rather differently constructed from those of *M. nemorivagus*, the hoofs being very much shorter, the interdigital cleft on the front of the pastern deeper, and the interungual web shallower. On the hind foot the glandular pocket was capacious and deep, extending backwards and upwards and touching the skin of the posterior side of the pastern just below the false hoofs. It was nearly elliptical in section, the lumen of the sac being larger than the orifice. Just below the orifice the integument formed an arched curve down to the strong heel-tie. The walls of the pouch were thickly and uniformly covered with long hairs projecting towards the orifice; and the walls of the interdigital cleft and the heel-tie were also covered uniformly with hairs. An olive-brown glandular secreting layer enveloped the pocket and extended inferiorly nearly to the heel-tie. On the front foot the pocket, although small as compared with that of the hind foot, was better marked than in any species of Deer I have examined with the exception of *Dorcelaphus americanus*, consisting of a very definite hair-lined invagination. Below the orifice the skin of the anterior surface of the pastern passed towards the hoofs in a direction parallel to that of the posterior side of the pastern, then descended obliquely downwards and backwards to the heel-tie, which for a short distance was hairless, thus differing from the corresponding area in the hind foot, and recalling the similar difference between the two feet of the Muntjacs (*Cervulus*).

Since pedal glands essentially similar in structure and position are found in such widely-divergent genera of Telemetacarpal Deer as *Rangifer*, *Capreolus*, *Dorcelaphus*, and *Mazama*, it may be inferred that they are present at least upon the hind feet in the

other Deer of this group, the genus *Pudu* alone constituting an exception.

Text-fig. 140.



A. Median vertical section of front foot of *Mazama bricenii* ♀.

B. Do. of hind foot of the same.

C. Do. of hind foot of *Dorcelaphus americanus* from specimen in the Museum of the Royal College of Surgeons.

I have had no opportunity of examining the feet or fresh skins of any examples of the following types of Telemetacarpal Deer. The principal external features of the glands will be found described in Mr. Lydekker's monograph.

Genus EUCERVUS Gray.

EUCERVUS HEMIONUS Raf.

(The Mule Deer.)

Nothing, so far as I am aware, is known of the structure of the feet; but the preorbital, tarsal, and metatarsal glands are present, the metatarsal gland being unique in its length, since it extends at least halfway down the cannon-bone towards the fetlock. This character I have used as a generic feature to distinguish *Eucervus* from *Dorcylaphus* (p. 971).

Genus BLASTOCERUS Sund.

BLASTOCERUS DICHOTOMUS Ill. (=PALUDOSUS).

(The Marsh-Deer.)

The preorbital and tarsal glands are present and the metatarsal gland absent, according to Mr. Lydekker. In this last-mentioned character the Marsh-Deer resembles *Mazama*.

BLASTOCERUS BEZOARTICUS Linn. (=CAMPESTRIS).

(The Pampas Deer.)

This species appears to resemble the foregoing in the nature of its glands.

The difference in the antlers suggests that this Deer should rank as a genus (or subgenus) distinct from *B. dichotomus*.

Genus HIPPOCAMELUS Leuck.

HIPPOCAMELUS BISULCUS Mol.

(The Chilian Guemal.)

Under the name *Xenelaphus*, Mr. Lydekker admits this and its ally *H. antisiensis* as a subgenus on account of the simply forked antlers, the coarse brittle hair, and the absence of the metatarsal gland. The latter, however, is also wanting in *Blastocerus* and *Mazama*, leaving the subgeneric status dependent on the character of the coat and antlers. This author also remarks that the simple form of the antlers is seemingly due to degradation and cannot therefore be regarded as an ancestral type, because the absence of spots in the fawn and the suppression of the metatarsal gland are obviously specialised features. Yet there is no commoner morphological phenomenon than the association of primitive with specialised features in a species. Moreover, the antlers of *Hippocamelus* and *Mazama* may be due to simplification from a much more complex type and yet be "ancestral" in the sense that their characters result from the retention to maturity of an early growth-stage.

Genus *PUDU* Gray.*PUDU PUDU* Mol. (The Chilean *Pudu*.)

I have had no opportunity of examining any material of this genus beyond the dried skins in the collection of the British Museum. According to Flower (P.Z.S. 1875, p. 160), the preorbital gland in *P. pudu* "is a distinct involution of thickened integument . . . with an aperture half an inch in length," and the pedal glands are not represented by distinct pouches, "but the skin in the depression between the toes on the dorsal surface of all the feet is bare and evidently has a free sebaceous secretion," representing, in the author's opinion, "the most rudimentary or earliest stage of an interdigital gland" (see p. 978). So far as it is possible to form an opinion from this description, it may be inferred that the interdigital depression in this aberrant genus closely, and it must be admitted surprisingly, resembles that of such species as *Cervus elaphus* or *C. eldi*.

Lydekker says both tarsal and metatarsal glands are absent ('Deer of all Lands,' p. 307).

The Classification of the Cervidæ.

From the account just given of the cutaneous glands of the Deer, it may be inferred that I think Sir Victor Brooke's classification of this family is correct, and Mr. Gordon Cameron's incorrect in the particulars in which it differs from Brooke's. It is important to refer to this matter, because in Mr. Lydekker's volume on Deer, to which recent authors not unnaturally refer as a standard work, Brooke's classification is set aside in favour of Cameron's, which gives primary importance to the antlers as a basis for the major divisions of the Cervidæ*.

Briefly stated, Mr. Cameron classifies the Deer into four groups:—(1) *Rangifer*, with antlers in both sexes; (2) *Alce*, with antlers rising laterally on the sides of the skull; (3) mostly American Deer of small or medium size, termed collectively *Cariacus*, with which are associated *Capreolus* and *Elaphurus*, a section characterised by "forked" antlers without a brow-time; (4) all the Deer of the Old World, except those mentioned above, including *Cervus* and *Cervulus*, which are distinguished by antlers consisting of a "beam," usually itself branched with a basal "brow-time." These third and fourth sections are, however, derivable from a common stock, from which *Rangifer* and *Alce* are excluded as "strangers to one another and to all other groups from the time when antlers first distinguished the family" (The 'Field,' 1892, p. 703).

Rangifer is considered to be a primitive type on account of the occurrence of antlers in both sexes and their early appearance in

* The 'Field,' 1892, pp. 625, 703, 741, 860. In the 'Field' for 1910, pp. 154, 215 (July), this classification was upheld by Mr. Cameron in opposition to the views advocated in this paper and summarised in the 'Field,' 1910, p. 97 (July).

the young. This assumption I believe to be false. If true, we should expect to find antlers of a primitive type in *Rangifer*. This, however, is not claimed, Mr. Cameron describing those of the Caribou "as the most specialised of existing antlers." Yet their fundamental resemblance to the antlers of the Deer, in which these weapons are well developed, is clear enough; and this fact is difficult to explain in conjunction with Mr. Cameron's double claim that the antlers of *Rangifer* are highly specialised and that the genus has followed a line of its own in evolution, independent of all existing species. The characters of *Rangifer* are, in my opinion, much more easily interpreted on the hypothesis that the genus is a specialised representative of the Dorecelaphine (Cariacine) Deer.

In the case of *Alce*, the lateral direction of the antlers is admittedly a peculiarity; but it is as obviously a derivative, not a primitive, feature. As for the antlers themselves, they are, in their simple form, clearly referable to the so-called "forked type" characteristic of Mr. Cameron's third section of Deer; and *Alce*, like *Rangifer*, may be best interpreted as a specialised member of that group.

Mr. Cameron also claims some support for his view of the great antiquity of these two Deer on the ground of their wide range in space; but although it may be true, very broadly speaking, "that types which have a wide range in time have also a wide range in space," there are probably no species in the world to which this remark applies with less force than it does to those inhabiting subarctic latitudes. For it is known that in comparatively recent geological times subarctic regions formed a continuous tract of land with similar physical conditions, offering no barrier to the eastward or westward migration of the indigenous species adapted to the surroundings.

The antlers of Mr. Cameron's third group (*Cariacus*, *Capreolus*, *Elaphurus*) are derivable, using his own words, from antlers consisting of a "forked beam with equal or subequal prongs," the Neotropical Guemal (*Hippocamelus*) being cited as an illustration; while the antlers of his fourth group (*Cervus*, *Cervulus*) are derivable from an "unbranched beam with a true brow-tine."

The terminology here employed is apt to confuse the issue. It suggests a fundamental difference between the two types of antlers described, whereas, on the face of it, it appears that Mr. Cameron is describing in different words structures which are to all intents and purposes identical. An "unbranched beam with a brow-tine" and a "forked beam" are alike describable as biramous antlers consisting of an anterior and a posterior prong arising from a common base, the anterior branch of the "forked beam" corresponding to the "brow-tine" and its posterior branch to the so-called "beam." Until this suggested homology be disproved, Mr. Cameron's assumption of the fundamental diversity of the two types of antlers cannot be regarded otherwise

than as an interesting speculation; and his conclusions are open to the criticism of being based upon premises which cannot, on the evidence, be accepted as firmly established.

Looking at the antlers of an adult Red Deer, Wapiti, Barasingha, Thameng, or Japanese Deer, it seems absurd to claim that the "brow-tine" is equivalent to the so-called "beam" which constitutes the rest of the antler. It appears merely to be the lowest of the series of branches which arise from the beam and to be comparable to those that are above it. The accepted terminology of the tines bears out this interpretation. I believe, nevertheless, that the "brow-tine" and the "beam" are respectively the anterior and posterior branches of an originally subequally biramous or dichotomous antler, like that, for instance, of the Guemal (*Hippocamelus*), and that their real equivalence in the Deer above-named is obscured by the immense development and complex armature of the posterior branch. It is this growth of the posterior branch at the expense of the anterior which characterises the antlers of most of the Deer of the Old World. A marked approach to this inequality is seen in the Reindeer, but in this genus the fundamental equivalence between the two branches is more apparent. Limitations to the growth of the anterior branch are imposed probably by necessities of feeding. If the anterior branch projected beyond the muzzle, a Stag could not feed with freedom off the ground; and even if it were prolonged obliquely upwards over the face, it would be a hindrance to browsing. No such limitations exist in the case of the posterior branch.

Support for the hypothesis that the antlers of the so-called Elaphine group were originally biramous like those of the Guemal (*Hippocamelus*), and that the biramous antler was preceded in evolutionary development by an unbranched antler such as is retained in *Mazama*, is supplied by the annual growth of an individual antler. The antler first appears as an undivided bud corresponding, I conceive, to the unbranched antler of *Mazama*. This bud then gives off an anterior and a posterior branch. For a longer or a shorter time these grow with equal rapidity, forming a biramous antler which in species with the anterior branch inclined upwards, as in the Axis, Sambar, or Japanese Deer, is shaped like a short-stalked Y, resembling, in fact, the permanent antler of the adult Guemal (*Hippocamelus*).

These stages are not equally evident in all Stags. In *Cervus* itself, for example, the early appearance of the "bez"-tine makes the biramous appearance of very short duration; but in the Thameng or Panolia Deer (*C. eldi*) the anterior and posterior branches grow at the same rate until the anterior branch has reached nearly its full size. Thereafter the posterior branch rapidly surpasses it and, increasing in length, develops its supplementary tines.

If this view of the fundamental resemblance underlying the antlers of all Deer be correct, it minimises the difficulty of

classifying *Elaphurus* with the Elaphine Deer, where Brooke, in my opinion, correctly placed it. For, according to this reading of the facts, the antlers of *Elaphurus* have not passed far beyond the biramous stage, seen transitorily but quite clearly in the growing antlers of such Deer as *Rusa*, *C. (Panolia) eldi*, and others. The peculiarities of the antlers of *Elaphurus* consist in the lengthening of the basal portion, the lengthening and bifurcation of the anterior branch which concomitantly has a strong upward trend so as to clear the face, and development of the posterior branch into a long slender usually undivided tine.

I suggest this homology of the anterior and posterior branches of the antlers of *Elaphurus* with the so-called "brow-tine" and "beam" of the antlers of the Elaphine group, because this Stag has evidently been the stumbling-block in the way of the acceptance of Brooke's classification both to Mr. Cameron and Mr. Lydekker. The latter, indeed, writes strongly on the point. He says: "If antlers count for anything in classification . . . the genus [*Elaphurus*] has nothing to do with any of the living Old World Deer with the exception of the Roes, while its alliance with the American Deer seems close" ('Deer of all Lands,' p. 234). Of course, antlers count something in classification; but whether they count as much as Mr. Cameron and Mr. Lydekker believe is quite another matter. In my opinion they do not; and I think the resemblance between *Elaphurus* and the American Deer, or at all events some of them, consists in the fact that the antlers in both have been specialised to a comparatively small extent beyond the biramous stage, which was, I believe, common to all Deer after the one-pronged or mazamine stage was passed. I do not think it can be claimed that such a resemblance is strong evidence of affinity.

Adopting, then, as a basis for the classification of the Cervidae the skeletal characters pointed out by Mr. Garrod and Sir Victor Brooke, I give the subjoined analytical key of what appear to me to be unquestionably valid genera tested by the feet and glands alone. Of course, I speak on this point with reserve as regards the American forms like *Hippocamelus*, *Blastocerus*, and *Eucervus*, which I have not seen. Very possibly there are more genera to come into his section than I have admitted. Of the Deer of the Old World I am more confident. It must be remembered, however, that the genera of this family have been established for the most part upon characters other than those forming the subject-matter of this paper, the branching and mode of growth of the antlers being the principal one. I have not in all cases made use of these characters because they are well known and have been repeatedly described.

In the preceding pages I have, without prejudice, adopted such names as *Hyelaphus*, *Rucervus*, *Panolia*, and *Pseudaxis* as connoting groups of subgeneric rank. I have, however, no confidence in the permanent admission of any of them as subgenera. In the future they will probably be granted full generic status; but this course or that of regarding them as subgenera or as synonyms

of *Axis* and *Cervus* will depend upon the views of each individual taxonomist. The point I wish to emphasise is that the characters on which they were established have not, in my opinion, so high a systematic value as those to which full generic importance is here attached. I do not, for example, think that in the future *Dama* will be set down as a subgenus of *Cervus*, whatever course may be adopted with regard to *Rucervus*, *Panolia*, or *Pseudaris*.

- α. Distal portion of lateral metacarpals persistent, interungual integument, where known, thickly hairy. (*Telemetacarpalia*). CAPREOLINÆ
 β. Naviculo-cuboid and external cuneiform bones of tarsus united; no pedal, tarsal or metatarsal glands *Pudu*.
 β'. Naviculo-cuboid and external cuneiform bones of tarsus separated; pedal glands present at least on the hind feet (? in *Eucervus*, *Blastocerus*, *Hippocamelus*); tarsal or metatarsal gland, sometimes both, present.
 c. Vomer dividing the posterior narial aperture.
 d. Rhinarium large; hoofs narrower, tied together posteriorly or throughout their posterior half; pasterns not depressed behind.
 e. Metatarsal gland very long *Eucervus*.
 e'. Metatarsal gland normal or absent.
 f. Metatarsal gland present; a large pocket-like pedal gland on the front as well as on the hind foot *Dorcylaphus*.
 f'. Metatarsal gland absent; at most a small glandular pocket on the front feet (? in *Blastocerus* and *Hippocamelus*).
 g. Preorbital glands moderately large; antlers branched. *Blastocerus*, *Hippocamelus*
 g'. Preorbital glands small; antlers unbranched *Mazama*.
 d'. No rhinarium, muzzle hairy; hoofs broad, widely separable at the heels, owing to the anterior position of the web; pedal glands on the hind feet only, and consisting, as in *Mazama*, *Dorcylaphus*, and *Capreolus*, of a deep pocket opening high up the pastern; tarsal and preorbital glands large *Rangifer*.
 e'. Vomer not dividing the posterior nares.
 h. Pedal gland either a deep and long interdigital cleft or a large pouch with constricted orifice on the hind foot; rhinarium large; no tarsal gland.
 i. Pedal gland a large pouch, with constricted orifice opening high up the pastern; preorbital gland absent; metatarsal gland present *Capreolus*.
 i'. Pedal gland a deep interdigital cleft, the hoofs united at the heels by a fold of integument; preorbital gland present; metatarsal gland absent *Hydropotes*.
 k'. Pedal gland a comparatively small invagination situated as in *Capreolus* and *Rangifer*; rhinarium very small; tarsal and preorbital glands present; metatarsal gland small or absent *Alce*.
 α'. Proximal portion of lateral metacarpals persistent or occasionally wanting. (*Plesiometacarpalia*). CERVINÆ
 k. Tarsus with naviculo-cuboid and cuneiform bones united; pedal gland a deep cleft on the hind feet; hoofs united only at the heels *Cervulus*, *Elaphodus*.
 k'. Tarsus with naviculo-cuboid and cuneiform bones separated.
 l. Hoofs of hind feet united only at the heels by a close fold of skin; the gland a long and deep hair-lined interdigital cleft as in *Cervulus*; a moderately deep cleft also on the pastern of the front foot *Dama*.
 l'. Hoofs of hind feet united almost throughout their basal depth by a deep interungual web; no deep cleft on pastern of front foot.
 m. Pedal gland a long and moderately deep cleft on the pastern of the hind feet; metatarsal gland naked, overlapped by marginal hairs *Axis*.

- m'*. No specialised gland or deep cleft on front or hind feet; metatarsal gland overgrown with hairs, occasionally absent; interungual integument naked.
- n*. Rhinarium extending some distance beneath the nostrils, as in *Aris*; tail long.
- o*. Tail bushy; antlers with short base, short undivided anterior branch and long, stout, two-pronged posterior branch..... *Rusa.*
- o'*. Tail tufted; antlers with long base, long, usually two-pronged anterior branch, and long, slender, usually undivided posterior branch..... *Elaphurus.*
- n'*. Rhinarium extending only a short distance below the nostril; tail (except in *Pseudaxis*) quite short..... *Cervus.*

Family CAMELIDÆ.

(Text-fig. 142, A, p. 981.)

According to Ogilby, Camels and Llamas have neither preorbital, inguinal, nor interdigital glands.

I have had no opportunity of examining fresh examples of either species of *Camelus*, but, according to Max Tempel, *C. dromedarius* has specialised glands in the interdigital cleft of both the front and hind feet. In the foot of a *Vicuna* (*Lama vicugna*) that died in the Gardens I found the pedal glands to be as well developed as in some Cervidæ, in the sense that the integument of the interdigital cleft secreted a strong-smelling substance. The hairs on the front of the pastern passed about halfway down the walls of the cleft, leaving the deeper half quite naked. In the specimen examined this naked area was covered with brown sticky substance smelling exactly like the urine of *Mus musculus*. The depth of this cleft is due to the fact that the integument of the back of the pastern, which extends to a point halfway between the heel and the nail of the hoof, is closely folded back upon itself, forming a shallow but long interdigital web.

The peculiarity of the foot of the Llama as compared with that of the Bovidæ is the small size of the nail and the length of the sole and of the heel as compared with it. The apex and lower edges of the nail, however, extend for a short distance on to the plantar aspect of the foot.

From the remark in Flower and Lydekker's 'Mammalia' (p. 295) that there is "a broad cutaneous pad, forming the sole of the foot, on which the animal rests in walking, instead of on the hoofs," one might be led to infer that the manner of walking in the Camelidæ differs essentially from that of other Ruminant Ungulates in that the latter walk upon the nails and the former upon a cutaneous pad behind the nail. This is not the case. All the ruminant Ungulates the feet of which I have examined, with the single exception of the Klipspringer (*Oreotragus*), walk upon the cutaneous pad forming the sole and heel of the hoof, and upon more or less of the inferior edge and apex of the nail in front. The Camels form no exception to this rule, the only difference being that the small nail does not invade the area of the sole to anything like the same extent, and that the sole and

the heel are continued farther backwards. In other words, it is only a difference in the degree of development of the parts composing the distal portion of the foot.

As is well known, the plantar area of the hoof in late foetal and many, perhaps all, newly born Cervidae and Bovidae is quite soft right up to and in some cases beyond the apex of the nail. This terminal portion soon shrivels and hardens, and becomes, in most cases at all events, indistinguishable from the inferior portions of the nail, especially externally; but usually the line of demarcation between the nail and the sole can be quite easily detected, especially on the inner aspect of the hoof, showing that the sole, although hard and horny, still persists and forms with the heels the main area of support during progression. The one exception to this rule known to me is the Klipspringer, which appears to support itself entirely upon the truncated apex of the nail of the hoof, with possibly a small piece of the hardened sole wedged in the angle formed by the two sides of the nail.

The males both of *Camelus dromedarius* and of *C. bactrianus* have a pair of well-developed glands on the summit of the neck just behind the occiput. In the living animal these may be easily felt as a pair of oval or roundish lumps lying close together. The hair overlying them has no underwool. In a male of *C. dromedarius* I have seen black watery secretion running from these glands and dropping off the hairs like sweat. This was in the month of June, when the glands of a male *C. bactrianus* were quite inactive. In the latter animal the glands were active and giving off a powerful repulsive odour much earlier in the year—that is to say, in March. The smell of the secretion from the glands in the Dromedary was equally repulsive, but reminded me of no substance in particular. It stains the skin of the fingers in much the same way as walnut-juice does. The position of the glands in the Dromedary is easily seen by the post-occipital patch of black hair. I have had no opportunity of observing the gland in the female Dromedary; but in the female Bactrian Camel it is much smaller than in the male, and never apparently noticeably active as it is in the latter when rutting.

Function of the Glands.

I do not know who first propounded the theory that the use of the cutaneous scent-glands in Ruminants is to keep the individuals of a species together. As early as 1836 Owen discussed this view; but, finding that the glands were present in some species of Antelopes of solitary habits and absent in some gregarious forms, he dropped this hypothesis as untenable. He does not appear, however, to have attached sufficient importance to the mutual need of discovering each other on the part of the sexes of solitary species at the breeding-season, nor to the necessity of the mother and young being together, at all events

periodically, in the course of the day. A hind, for example, which leaves her newly dropped fawn in the jungle or bush while she is away feeding, must have some means of retracing her steps to the spot; and it may well be that she does so by means of the scent her own foot-tracks have left.

This obvious criticism of Owen's reasons for rejecting the theory has no doubt suggested itself to others; for the view that the secretion of the scent-glands serves to guide individuals of a species, whether gregarious or not, to one another appears to be commonly held, and was clearly expressed by Flower and Lydekker in their volume on the 'Mammalia' (pp. 315-316). That the secretion from the pedal glands must scent the ground over which the animal passes seems clear, for the pouch is commonly furnished with long hairs projecting from the orifice or the edge of the orifice, and the function of these hairs seems to be to guide the secretion downwards between the hoofs. Similarly the substance secreted by the tarsal, metatarsal, and carpal glands would touch against higher herbage, and might leave a taint behind. But the position of these glands suggests that their function is also to indicate where the animal has been lying. In the habitual resting attitude of Ruminants, the area below the knee (carpus) on both the front legs is pressed to the ground, and in the case of the Cervidae the metatarsal gland on the outside of one hind leg and the tarsal gland on the inner side of the other in the same way come simultaneously into contact with the soil whether it be bare or overgrown with vegetation. Now the Deer which possess these glands on the hind legs have no inguinal pits or knee glands. Conversely the Bovidae, which have no tarsal or metatarsal glands, not uncommonly possess inguinal pits and sometimes knee glands. The suggestion, therefore, is obvious that the inguinal pits of Sheep and many Antelopes, so-called, represent functionally the tarsal and metatarsal glands of the Deer and scent the ground where the animal has been lying.

It is clear that the above proposed explanation of the use of the inguinal and crural glands applies equally well to species which inhabit jungle, plain, sandy desert, or barren mountain heights. It is therefore more satisfactory than the view that the scent of the secretion is only left behind on the vegetation by the animal's passage through it. Sheep, for example, which possess inguinal glands, frequent hilly country, feeding on grass often not high enough to reach the inguinal region. Except, therefore, when these animals are in a state of repose the secretion of these glands can seldom be left behind adhering to natural objects. It is also likely that one individual can follow another or detect his whereabouts by the wafting of the scent through the air, irrespective of contact with the ground. This wafting of scent is probably the sole function of the caudal glands of Goats (*Capra*), which can in no circumstances dispose of their secretion by contact with the soil, unless a certain amount of it falls to the ground sticking to the faeces. Be it noted, too, that the habit of turning

up the tail in flight, so common in Ruminants, would expose the secretion of these glands to the air.

It has also been suggested, by Owen for example, that the use of the secretion of the pedal glands is lubrication of the hoofs. This is possible. The suggestion, however, does not exclude the explanation advocated above; and it appears to me to be probable that the function of the secretion of the pedal glands is the same as that of the carpal, tarsal, and metatarsal glands, which cannot be for lubrication. In this connection it is significant that *Epyceros* and *Tetraceros*, which have no pedal glands, have very specialised glands on the hind legs, occurring in the former above and in the latter within the false hoofs, in situations, that is to say, where the secretion must taint the ground where the animal lies.

There is a good deal of evidence that the preorbital gland has a sexual significance, at all events in part. Bennett, for example, noticed that an immature example of *Antelope cervicapra* had the lips of the sinus small and closely applied, so as to hide entirely the internal lining of the sac. In a full-grown animal, on the contrary, the sac, under the influence of excitement, was everted so as to form a projection rather than a hollow. At such times the animal delighted to rub the sac against any substance offered to it, loading it with the secretion, which had a slightly urinous odour. In a castrated individual, believed to be about the same age as the last, the gland, on the contrary, was only developed to the same extent as in the young male and was never everted as in the normal adult buck (P. Z. S. 1836, pp. 35-36). Hodgson also believed that in the Serow (*Capricornis thar*) the gland was "connected with the generative organs"; for he noticed that, in the spring especially, a thin viscid secretion was constantly poured out from the sinus, and he suggested that this profuse secretion was a means of relieving the animal during the time of extraordinary excitement to which it is liable in the breeding-season (P. Z. S. 1836, p. 39). Max Weber, moreover, has collected a good deal of evidence showing that the preorbital gland is better developed in the male than in the female of the many species of Antelope. I have noticed this myself in the case of *Raphiceros campestris* and *Tetraceros quadricornis*. I have also observed the glands of the latter species enlarge and discharge copiously in the summer, and those of specimens of *Gazella rufifrons* and *Cephalophus dorsalis* to be markedly swollen at that season. I have also seen them discharging actively in July in a female example of *Sylvicapra grimmii*, and to be quite inactive in the same animal in August. Moreover, in some Deer (*Pseudaxis* and *Rucervus*) I have noticed—and this is possibly true of all Deer—that the preorbital gland is quite small and shallow in the young as compared with the adult, a fact warranting the conclusion that this gland attains its greatest size and activity with sexual maturity.

But I cannot, on the evidence, bring myself to believe that the significance of the preorbital gland is wholly sexual. It is certain,

for example, that the gland is in some cases under the influence of other emotions than that of sexual excitement. A male Black-buck, for instance, advancing upon a man with hostile intent, turns up his tail, and everts the gland to its fullest extent; and I have seen a Sambar stag with ears pricked, nostrils dilated, and gland completely everted, gazing intently at a cat crossing the yard, his whole attitude forcibly suggestive of curiosity and doubt with a strong admixture of fear.

The habit of rubbing the secretion of the preorbital gland against the bars of cages or other objects was recorded by Bennett of *Antelope cervicapra*, by Ogilby* of a species of Gazelle, and by Mr. Beddard† of *Oreotragus*. Ogilby, indeed, speaks of this act as frequent. In my experience it is uncommon. I have only noticed such behaviour in one Antelope, an immature example of Maxwell's Duiker, which invariably rubbed its gland against my proffered hand, exactly as a cat rubs its mouth and cheek. Considering the immaturity of the specimen in question, I cannot believe that sexual excitement was in any sense the cause of the action. It may therefore be the case, as Ogilby suggested, that "rubbing the crumens against the shrubs or stones of their desert and mountain habitats . . . may serve to direct [Antelopes] in their wanderings and migrations, when the storms and fogs incident to such places obscure all visible landmarks." As guide-marks, therefore, appeal to the sense of sight and enable the members of a species to follow one another and keep together when vision is unobstructed, so, it is believed, do the scent-glands described in this paper serve the same purpose by appealing to the sense of smell when, for any reason, free vision is prohibited.

It would be idle, however, to pretend that this hypothesis gives a full explanation of the use of the glands. It fails, for example, to account for the fact that in many, perhaps all, cases each gland emits its own peculiar scent, as recorded, for instance, of a Muntjac (*Cervulus*) and of a Gazelle (*G. dorcas*). That each scent tells its own tale to other members of the species, it is almost impossible to doubt; but what that tale may be, I am wholly unable to surmise.

Origin and Evolution of the Glands.

The preorbital glands in all the Cervidae, and in the majority of Bovide that possess them, consist of an integumental thickening forming a larger or smaller invaginated sac, which serves to store the secretion. But in a few of the Bovidae, like the Duikers (*Cephalophus*), the Gnu (*Connochates* and *Gorgon*), Buffon's Kob (*Adenota kob*), and the Sable Antelope (*Hippotragus niger*), there is no invagination, the secretion making its way directly to the exposed surface of the skin. The simplest type of preorbital

* P. Z. S. 1840, p. 9.

† 'Mammalia,' The Cambridge Natural History, p. 13 (1902).

gland known to me is found in Buffon's Kob (*Adenota kob*) and the Sable Antelope (*Hippotragus niger*). The skin of the secreting area is merely thickened and retains its normal hairy clothing. The hairs, however, are long, forming a tuft or mat and are stuck together or hold the secretion like a scurfy powder. It is a natural inference that all the preorbital glands, however specialised, arose from simple integumental thickenings, with enlarged sebaceous and sweat-glands, resembling in essence that found in the Sable Antelope.

Exactly similar to this and equally simple in structure are the carpal or knee-glands of some Antelopes, like Gazelles and their allies, and of some Sheep, the tarsal or hock-glands of the Telemetacarpal Cervidae, and also the metatarsal glands of Deer belonging to both the divisions of this family. In some species of Deer (*Axis axis* and *porcinus*) the glandular area itself is naked and is overlapped by a fringe of long hairs surrounding it. A further stage in the evolution of this kind of leg-gland is found in the Pallah (*Epyceros*), where the glandular layer is restricted to the periphery of the area, forming an elevated ridge round it, the secretion accumulating on the smooth skin thus circumscribed.

In connection with the inguinal glands it is noticeable that they are intimately connected with the mammae. In the majority of cases their orifices are situated close to those organs, and the deepest part of the pocket actually overlies them; and when, as in *Pantholops**, the orifice is remote from the mamma on each side, the invagination is elongated so as to extend inwards as far as the area overlying the mamma. Again, two pairs of inguinal pouches are found only in species which have two pairs of functional mammae (*Tragelaphus*, *Redunca*).

These facts suggest that the secretion found in the inguinal sacs is derived actually from the mammary glands. This I believe to be the case; and the view is corroborated to a certain extent by the fact that the secretion in the sacs not uncommonly has an unmistakable odour of cream-cheese, or sour milk. The presence of inguinal glands in both sexes cannot be alleged as an objection to this supposition; for mammary glands are found in males as well as in females, although they are normally inoperative in the former.

It seems to me that for the origin of the pedal glands we must look to one of two processes: that is to say, they have either arisen as invaginations of the interdigital integument of a more or less fully webbed compact foot, such as is seen in *Bos*, *Taurotragus*, *Pantholops*, *Epyceros*, and others; or they are the remnants, larger or smaller according to the genus, of a primitive interdigital space.

The former explanation appears at first sight to be the more probable; and from the remark made by Flower as to the

* But not in immature examples of *Sylvicapra*.

seemingly primitive nature of this gland in *Padu*, I infer that this was the view he held. If this be so, the shallow or short pocket seen in such genera, for example, as *Alce*, *Redunca*, and *Pseudois* preceded, in an evolutionary sense, the well-developed gland possessed respectively by such genera as *Capreolus*, *Pelea*, and *Ovis*. Further, it will follow as a possibility, perhaps as a probability, that the pedal glands have been developed independently more than once in various groups of Bovidae and Cervidae; and that the genera within these families characterised by pasterns without any interdigital space have an earlier form of foot than those in which such a cleft is found: that the hind foot of *Cervus*, for instance, to take a concrete case, is more primitive than that of *Dama*.

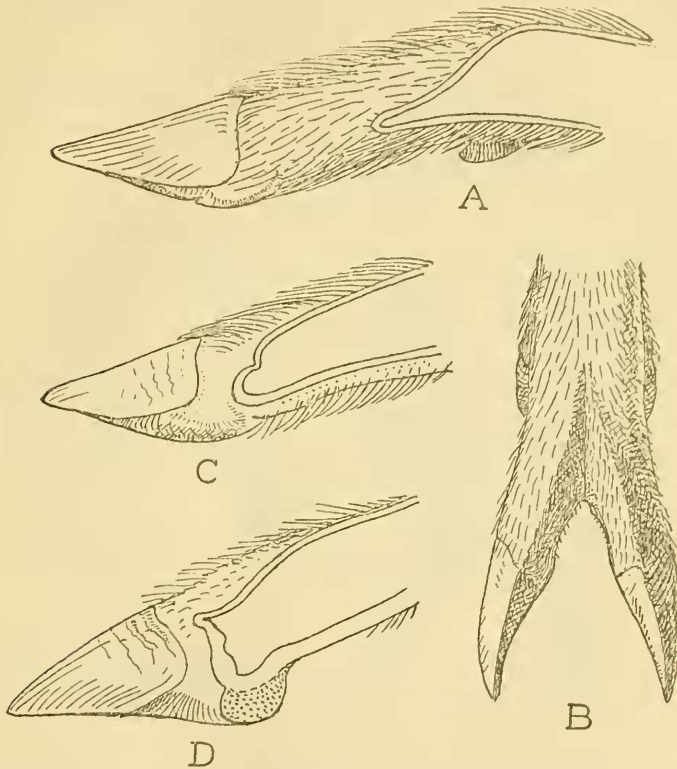
I believe this view to be erroneous; for everything we know of the evolution of the feet in Ruminantia points to the conclusion that their structural peculiarities are due to descent from four-toed feet with the phalanges separated to a greater or less extent. Gradually the lateral digits became shortened, raised from the ground, and practically functionless so far as affording support to the body was concerned. The weight was borne by the two middle toes, which became gradually strengthened for the purpose by the extension of the integument between them. Now when Mammalia of other groups develop an interdigital integument or "web," this web always, I believe, extends along the posterior or inferior aspect of the toes, leaving more or less of a cleft between them in front or above. This is well shown in such forms as *Lutra* and the Canidae and in various amphibious genera of Rodents and of other orders. For these reasons I believe that the earliest type of Ruminant foot is that in which the interdigital web consists of a fold of integument extending along the back of the pastern only, leaving a wide and deep depression between the bones above the hoofs in front. But when two surfaces of skin are opposed to form a cavity or crease, conditions favouring the activity of the skin-glands, or at all events conditions preventing the evaporation of integumental secretions, are set up. Hence, in a foot with a posterior web holding the digits together behind and a cleft between them in front, we have conditions conducive to the development of a scent-gland; and I conceive that it was from a foot of this structure, containing a potential pedal gland, that the various types of feet of the Ruminantia, whether containing glands or not, have been derived, and that the glandular pockets, whether large or small, are the remnants, specialised for the secretion of scented material, of a primitive anterior interdigital cleft.

This conception seems to me to supply the most satisfactory explanation of the prevalence and diversity of the pedal glands of the Ruminantia, all the glands being thus traceable to a common origin.

Of existing forms of this group the most primitive type of foot is found in the Tragulina, itself a primitive group combining

characters of the Suidæ, the Camelidæ, and the Cervidæ. In specimens of *Tragulus stanleyanus* (or an allied form) and of *T. meminna*, which lived in the Gardens, I find that the web on the posterior side of the pastern consists of a fold of skin which stops short at a point about halfway between the false hoofs and the heels; the back of the pastern is open in its lower half, and its front is marked with a long triangular depression, the apex of which extends up to the level of the false hoofs.

Text-fig. 141.



- A. Median vertical section of foot of *Tragulus meminna*.
B. Anterior aspect of foot of *T. stanleyanus*.
C. Median vertical section of foot of *Dicotyles*.
D. The same of *Phacochærus*.

These feet are the only ones known to me amongst the Ruminantia in which the web ceases behind far above the heels. The inner walls of the two digits of the pastern are clothed with hair, which is short and scanty in *T. stanleyanus*, longer and less

scanty in *T. meminna**; but I could detect no trace of any secretion indicating special activity of the skin-glands of the surfaces in question.

In the Camelidæ, as exemplified by *Lama vicugna*, the foot is more specialised with respect to the extension of the web to a point halfway between the heel and the nail of the hoof; but the anterior depression on the pastern is very deep and long and glandular in its deeper portion, and the nail is small. (Text-fig. 142, A.)

Still more specialised is the foot in the Suidæ; for although there is a deeper or shallower depression on the front of the pastern, admitting of considerable distension of the hoof, the anterior and posterior walls of the pastern are widely separated and there is a strong deep interungual union extending forwards from the heels to a greater or less extent according to the species. In a Peccary (*Dicotyles collaris*) the heels were separable and the interungual union shorter and the anterior depression deeper than in a Wart-Hog (*Phacochoerus*), in which the depression was quite shallow and the interungual union long in comparison (text-fig. 142, B, D). In the foot of the Wart-Hog, moreover, which was kindly given to me by Rowland Ward, there was an actual horny union between the heels, which were thus quite inseparable. In both these species the interungual area was quite smooth; but I detected no trace of specialised glands†.

Reverting once more to the Ruminantia, I find, as is not surprising, that the foot of the Musk-Deer (*Moschus*) comes nearest to that of *Tragul*. The pastern-web of *Moschus* nearly reaches the heels of the hoofs but not quite; the feet indeed, apart from the wealth of hair that clothes them, are like those of *Tragul*, but very much shortened and having the glands of the depression active.

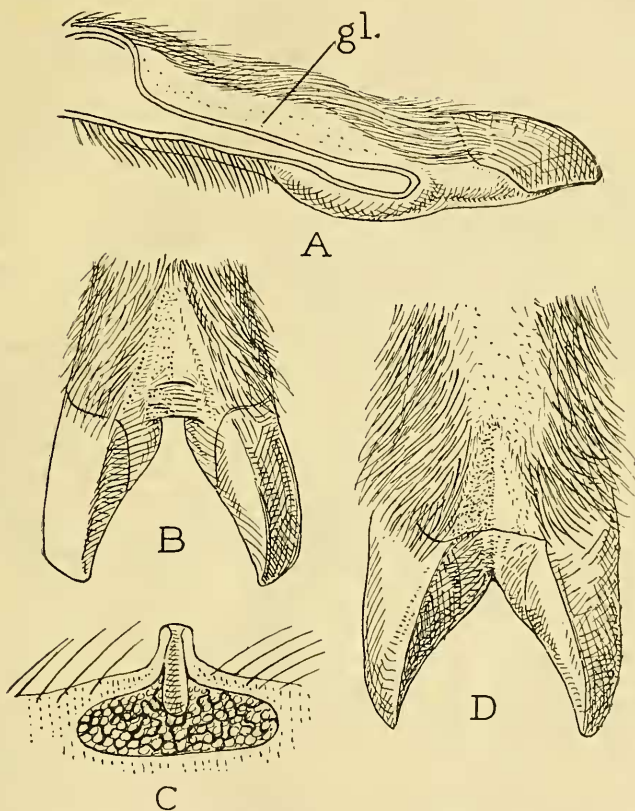
It is only a short step from the foot of *Moschus* to the hind foot of *Dama* or *Elaphodus*, the chief difference being that in these Deer the pastern-web extends right down to the heels, tying

* In *T. stanleyanus* also the skin of the back of the pastern is coriaceous and visible through the hairs, which are as scanty as on the inner surface of this part; whereas in *T. meminna* the skin is invisible on the back of the pastern when the hairs are undisturbed. I have not investigated the submandibular glands of *Tragul*.

† The secretion of the dorsal gland in both species of Peccary has a strong and pungent odour, like concentrated human perspiration. It may not be without significance that the scent of the South American Tree Porcupines (*Coendu villosus* and *prehensilis*) is exactly the same, as I have already recorded (P. Z. S. 1908, p. 946). And since this scent has, I believe, a warning significance in the Porcupines, it may be that we have here an instance of mimicry, Batesian or Müllerian, in smell. On the other hand, the function of the gland in the Peccary may serve the purpose merely of keeping the members of the herd together. Owen's figure and description of this dorsal gland in the Peccary are not very satisfactory. He describes and figures the gland as opening by an orifice in the mid-line of the back, without mentioning any nipple ('Anatomy of Vertebrates,' iii, p. 635, 1868). Possibly his preparation was not made from fresh material, for in the specimens I have examined the gland was marked externally by a conspicuous upstanding nipple. This was traversed by a central duct dipping into the lobular fat-like tissue of the gland. When the gland was squeezed, fluid secretion could be easily made to exude from the orifice at the summit of the nipple. (Text-fig. 142, C.)

them tightly together; and the upper portion of the interdigital cleft in front is deepened, showing the beginning of the differentiation of the glandular pouch. Hardly more advanced is the hind foot of the Muntjacs of the genus *Cervulus*, except that in *C. muntjac* part of the glandular area is markedly more pocket-like. A further stage is exemplified by the hind foot of the Hog-Deer (*A. porcinus*) and of the Axis Deer (*A. axis*), where the web

Text-fig. 142.



- A. Median vertical section of foot of *Lama vicugna*: *gl.*, glandular area.
 B. Anterior aspect of foot of *Dicotyles collaris*.
 C. Median vertical section of dorsal gland of the same.
 D. Anterior aspect of foot of *Phacochærus*.

extends further forwards from the heels, holding the hoofs more securely and tightly together, the interdigital cleft being shallower owing to the greater space between the anterior and posterior walls of the pastern-web. It is quite easy to imagine the steps by which the comparatively narrow pocket-like gland of *Mazama*, *Cervulus*, and *Rangifer* has been derived from a much longer and

shallower glandular depression such as is seen in *A. axis* and *A. porcinus*; and also on the other side how by the gradual shallowing of the depression in the feet of these last-named species the condition of things found in the feet of the Red Deer (*C. elaphus*) and its allies has been reached.

I do not by any means wish to suggest that the species named stand in the exact line of descent to one another; but I do think it probable that their pedal glands represent approximately the stages through which the various types of pedal glands met with in the Cervidæ have passed in their evolution.

Similar stages in the gradual obliteration of the interdigital space accompanied by the evolution of differentiated pedal glands and their final suppression may be traced in the Bovidæ. In *Madoqua*, *Raphicerus*, and *Cephalophus*, for instance, the digits of the pastern are held together by a long and close fold of integument constituting a web which extends down or nearly down to the heels; the anterior skin of this fold forms the posterior wall of the glandular interdigital cleft, as in *Cervulus* and *Dama*. This cleft is at first open below between the hoofs and remains so in *Madoqua* and *Cephalophus*. But in both these genera, as well as in *Raphicerus* and *Dorcotragus*, the orifice of the cleft is shortened to a greater or less extent, according to the species, by the downward extension towards the hoofs of the folded integument of the anterior surface of the pastern, forming a longer or shorter anterior wall to the enclosed glandular space. Another simple modification is seen in the Gazelles, in which, while the orifice of the cleft retains almost unchanged in its original length, its inferior portion is closed and shut off from the interungual space by the anterior extension of the posterior web from the heels to the front of the hoof. Practically the same structural change has taken place in the Oribi (*Ourebia*) and in the Hartebeests (*Bubalis*, *Damaliscus*), except that in *Bubalis* the anterior web overlaps the cavity to a considerable extent above and in front.

The adult White-tailed Gnu (*Connochates gnu*) exhibits a further stage in the evolution of the gland seen in the Hartebeest, the orifice of the cleft being still more shortened and the posterior integumental web not so closely folded. A further stage in the closing up of the orifice of the cleft is exemplified by the feet of *Oryx beisa*; and this is followed by the reduction of the orifice to a small circular aperture as in *Hippotragus*, *Pelea*, *Namorhedus*, and *Oris*; the final stage, sometimes certainly and always probably of sporadic occurrence within the limits of a species, being the retention of merely the orifice and part of the duct of the gland as in *Redunca*, *Capra*, *Hemitragus*, and *Pseudois*.

If this be the correct view of the evolution of the feet, there must be some reason or reasons for the disappearance of interdigital clefts. It seems certain that large interdigital clefts must be a source of weakness to the feet. Although a foot with its two component digits united by a close fold of integument extending from the heels up the back of the pastern is more suitable, on

account of its distensibility, for progression over soft and yielding ground than a foot with its component digits united by skin extending forwards from the heels to the front of the hoofs and restricting their separation, it is obviously less well adapted for supporting heavy weight, for speedy propulsion over hard unyielding ground, and for resisting the impact of a downward leap on a mountain side, on account of the liability to rupture of the integument under the strain put upon it.

Strengthening the feet, then, has probably been one of the factors, perhaps the principal factor, that has operated in favour of the reduction in size or total disappearance of the interdigital clefts. This theory helps to an understanding of the fact that, broadly speaking, large and heavily built Ruminants have small interdigital clefts or none, and that large interdigital clefts are for the most part found only in small animals. There are several marked exceptions to this, however, and no doubt other factors than the one suggested have influenced the formation of the feet, such as the use or uselessness of pedal scent-glands. For example, large Ruminants are much more easily kept in view by members of their own species than small ones; or, if they live in thick bush, are more easily followed by hearing as they crash away in a state of panic through the vegetation. Of these and other matters, however, we shall never have full knowledge until our information is much more exact than it is at present with respect to the senses and to the bionomics of the species concerned.

In the light of the above-made suggestions, the following considerations are worth bearing in mind :—

1. Giraffes are large, heavily built animals living in open woodland country and gallop with speed over rough uneven ground. The feet are compactly built and without interdigital clefts. The great height of Giraffes gives them considerable range of vision, enabling stragglers to keep with the rest of the herd. They can, moreover, only with difficulty and delay reach the ground with their nostrils. Hence specialised pedal scent-glands would be of little use to them for tracking.

2. All the species of *Bos* are heavily built, mostly large animals with thick legs. They live either in the open or in jungle or bush, and can be followed either by sight or by the sound they make passing through the foliage. The same applies to the Musk-Ox and to *Taurotragus*.

3. The Oryginæ (*Hippotragus*, *Oryx*) are also Antelopes of large or medium size and considerable weight. The interdigital cleft is reduced to a gland with a small orifice, which is the only break in the continuity of the integument of the anterior surface of the pastern; and the orifice is smaller in the larger *Hippotragus* than in the smaller *Oryx*.

4. In the Bubalinæ, large or medium-sized Antelopes, although the interdigital cleft is large and highly glandular on the front feet, it is reduced to a shallow depression on the hind feet. It is in the hind limbs that the galloping power principally lies; and

some of the Hartebeests, the Sassaby (*Damaliscus lunatus*), for example, are extraordinarily fleet of foot.

5. In the Cervicaprinæ, the larger species of *Kobus* and *Adenota* have no interdigital clefts or glands; only in the comparatively small and lightly built genus *Pelea* are the clefts retained in the form of saccular glands with a small orifice.

6. All the Duikers (Cephalophinæ) are of small or very small size and live in the forest on soft yielding ground or in fairly open country overgrown with scrub. They have large interdigital clefts and pedal glands, the scent of which is probably useful for tracking individuals concealed by the bush, through which they dive away when alarmed.

7. The Neotraginæ (*Raphicerus*, *Madoqua*, *Ourebia*) are also of small size and lightly built, and mostly frequent country overgrown with bush or scrub. They have large interdigital clefts and glands, by means of which one individual could silently follow by scent another hidden from view. *Dorcotragus*, on the contrary, lives on rocky hill-sides and has the hoofs shortened to lessen their spread at the tips, the heel-tie thickened to hold them tightly together, and the sole and heel modified to form a soft pad to break the force of a leap and prevent slipping, the interdigital cleft and gland being at the same time retained.

8. The Klipspringer (*Oreotragus*), commonly believed to be related to the Neotraginæ, although of small size and light weight, has lost the interdigital clefts. His habitat is rocky crags, where he leaps surefootedly from point to point, the hoofs although separable being firmly bound together by the thick interungual integument.

9. All the Antilopinæ (*Gazella*, *Antilope*, *Antidorcas*) live in the plains or more or less open country. They are, on the average, of small size, although larger than the Neotraginæ, and of light build, and depend for safety upon their great speed in the open. Although the interdigital clefts are large, the hoofs are held together by a fold of integument running forwards from the heels and restricting their spread to a greater extent than in the Cephalophinæ and, on the average, than in the Neotraginæ.

10. I do not know why *Ammodorcas* has lost and *Lithocranius* has retained the interdigital clefts, unless the explanation may be sought in the totally different modes of progression of the two Antelopes, which more than one observer has recorded. *Lithocranius* runs with a skulking action, ducking under the bush, with the head stretched forwards; *Ammodorcas*, on the contrary, moves with a bold stepping action, holding tail and neck erect. This at least suggests that the Dibatag is more easily kept in view by its companions than the Gerenuk, and has therefore less need of pedal scent-glands to indicate the direction taken.

11. In the Caprinæ the only wild forms which possess well-developed pedal glands belong to the genus *Ovis*, the others (*Ammotragus*, *Pseudois*, *Hemitragus*, and *Capra*) being without them. The latter differ markedly from Sheep in superior activity and in

their comparatively greater leaping powers, attributes which are correlated with a difference of habitat, the Goats and their allies habitually frequenting precipitous exposed rocky hill-sides or mountain heights rather than elevated plateaus intersected by ravines where Sheep are to be found. It seems to me probable that the ground frequented by Sheep is better adapted by its vegetation for holding the scent of the foot-glands and perhaps affords more cover for concealment, requiring tracking by scent, than the bare exposed situations to which the other genera are adapted.

12. In the Rupicaprinæ well-developed foot-glands occur in *Rupicapra*, *Næmoredus*, and *Capricornis*. The last two never seem to be found far from mountain forests, where individuals may easily lose sight of each other and need scent-glands to keep together. Although possessed of considerable activity and skill in covering rough ground at speed, they have not the climbing or leaping power of Goats. In this respect Chamois appear to equal Goats, and they have their feet strengthened by the forward extension of the interungual web, while retaining pedal glands which are useful perhaps in the mountain forests, where at certain times of the year Chamois resort. Although not apparently gifted with special activity or leaping power, *Oreamnos* inhabits localities right away from forests and bare of all but the scantiest vegetation. In this particular, as in the structure of their feet, they closely resemble Goats. Somewhat of a mountain-forest dweller like *Næmoredus* and *Capricornis*, *Budorcas* is nevertheless a comparatively inactive animal of large size and heavy build, requiring strong feet to carry his weight up and down the mountain-side.

13. In the Cervidæ, also, small and medium-sized animals have on the average larger interdigital clefts and more capacious glands than large animals. Very deep and long clefts with highly developed glands are found, for instance, only in small forms like *Hydropotes*, *Cervulus*, and *Elaphodus* and in the medium-sized *Dama*. Shallower but equally long clefts occur in the small *Hyelaphus* and the medium-sized *Axis*, the much larger *Rusa*, which is allied to both these genera, being devoid of them, as also are all the large Deer of the Old World. In the Telemetacarpal Deer, setting aside *Hydropotes*, there is almost always, so far as is known, a large pouch-like gland in the hind foot in genera ranging in size from the small *Mazama* to the large *Rangifer*, two exceptions being the diminutive *Pudu*, in which the glands are aborted, and the giant *Alce*, in which the gland is considerably reduced.

Very little is unfortunately known about the habitat of *Pudu* beyond the fact that it has been recorded from Ecuador and the Chilian Andes and appears to live normally at tolerably high altitudes. From its compactly built feet, I infer that this little Deer frequents hard or stony ground requiring firmly welded hoofs. If this be so, we find a reason for the disappearance of the glandular pouch in the feet found in its ally *Mazama*

if there is any truth in the supposition that such pouches are a source of weakness.

In the case of *Alce* the nearly vestigial nature of the pedal gland is accompanied by two features in this genus which have an interesting bearing on the suggestions here put forward to account for the retention or loss of interdigital clefts and glands. In the first place, this Deer is of great stature and weight, the latter requiring strong feet for support and the former making concealment from sight, involving the necessity of tracking by scent, less likely than in the case of smaller animals. In the second place, length of limb is correlated with shortness of neck, so that the Moose can only with difficulty reach the ground with its nose. Scent-tracks left by the feet, therefore, would be of comparatively little use in enabling one Moose to find another.

No Deer known to me have such strongly built completely webbed feet as are found in the large Bovidae like *Taurotragus* and *Bos*, or indeed as in some of the smaller members of that family, like *Tetracerus* and *Oreotragus*. Generally speaking, there is a greater tendency towards plantigradism and there is nearly always a more marked depression on the front of the pastern. This is to be attributed, I suppose, to the circumstance that Deer are for the most part denizens of woodland country, woods, jungle, or swamps, where the soil is usually softish and yielding. This brings us to the fact, otherwise perhaps seemingly opposed to the suggestion here made as to the cause conducing to the suppression of the pedal gland in the hind foot, that a large and heavily built animal like the Reindeer none the less retains a well-developed glandular pouch. The Reindeer, however, has a foot eminently adapted for traversing soft ground, whether it be snow or swamp, and does not require a foot of such strength as to call for the suppression of the glandular pouch.

That the Cervidae, like the Bovidae, originally possessed interdigital clefts and glands on the front as well as on the hind feet is probable on general grounds, and also from the fact that a gland is retained on the front foot in a state of greater or lesser development in some American Deer, while a moderately deep cleft is present on the front foot of *Dama*. The only suggestion I can at present make to account for the greater compactness of the fore feet as compared with the hind feet is the fact that all Deer, I believe, both stags and hinds, commonly use their fore feet both in attack and defence, dealing blows with great precision, swiftness, and strength. This I have myself witnessed on more than one occasion. For such a purpose it seems obvious that a strongly built foot is required.

These brief comments on the bionomics of Ruminants indicate in a general way the lines along which research, likely to lead to a better understanding of the structure of the feet and the reasons for the retention or loss of the pedal glands, may probably, I think, be pursued with profit.